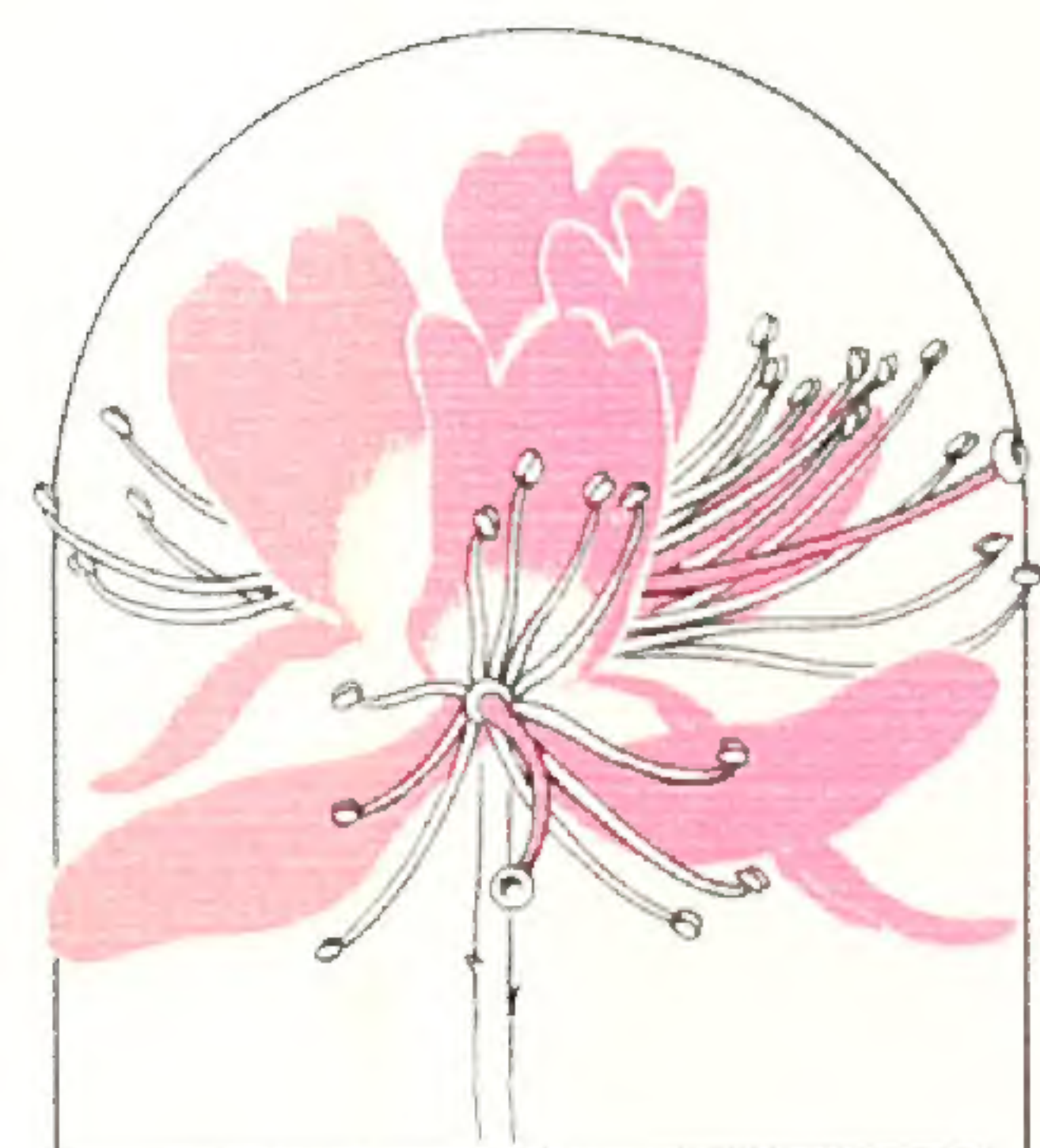




RHODORA

Journal of the New England Botanical Club

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RHODORA

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SEAWEEDS OF THE BRAVE BOAT HARBOR SALT MARSH AND ADJACENT OPEN COAST OF SOUTHERN MAINE

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ABSTRACT. A comparison of species richness at 51 coastal and estuarine sites in southern Maine is given, encompassing the area from Cape Neddick, York, to Fort Foster, Kittery, and including the Brave Boat Harbor salt marsh (York/Kittery). A total of 148 taxa was recorded, which is relatively high compared to other coastal or estuarine areas in northern New England. Seaweed populations exhibited three major distributional patterns: coastal (41%), coastal-estuarine (51%), and estuarine (8%). Perennial species dominated open coastal and outer estuarine locations, while annuals were most conspicuous at inner estuarine sites. Twenty-nine taxa were restricted to a single site (2% occurrence), whereas 19 were found at 21–36 sites (41–71% occurrence). Diversity in Brave Boat Harbor's main tidal channel was relatively high (83 species), presumably because of coastal and estuarine influences, diversity of habitats, and limited anthropogenic impacts. Six new or uncommon seaweeds were recorded from Brave Boat Harbor, including the invasive green alga *Codium fragile* subsp. *tomentosoides*, the green algal epiphyte *Urospora curvata*, the tubular opportunistic brown alga *Melanosiphon intestinalis*, the entangled or partially embedded ecads *Fucus vesiculosus* ecad *volubilis* and *F. spiralis* ecad *lutarius*, and a dwarf embedded moss or "muscoides-like" *Fucus*. The prolific growth of psammophytic populations of *F. spiralis* on sandy bluffs at Brave Boat Harbor is also unique, as it typically grows on hard substrata within contiguous muddy estuaries. It was most abundant in the outer third of the Harbor, along with its detached ecad *lutarius*. *Ascophyllum nodosum* ecad *scorpioides* and *F. vesiculosus* ecad *volubilis* grew commonly as detached or buried populations in the interior parts of the Harbor, while the "muscoides-like" *Fucus* was found on outer high sandy marsh surfaces.

Key Words: seaweeds, ecology, Brave Boat Harbor salt marsh, nearshore open coast, southern Maine.

Salt marshes in Maine are rather limited in both occurrence and areal coverage (Jacobson and Jacobson 1989; Jacobson et al. 1987). No major tidal wetlands occur within two of the state's largest embayments, Cobscook Bay in extreme eastern Washington County (an extension of the Bay of Fundy with wide-ranging tidal amplitudes and swift currents) and the sheltered Penobscot Bay region of Hancock, Waldo, and Knox Counties. Small, marginal tidal marshes occur from midcoastal Lincoln and Sagadahoc Counties to Casco Bay (Cumberland County). Further south, broad expanses of tidal wetlands in Scarborough, Wells, York, and Kittery are comparable to those of the Great Bay Estuary System of Maine and New Hampshire, the Hampton-Seabrook marsh in New Hampshire, and many large marshlands extending from the Merrimack and Parker Rivers to Cape Cod, Massachusetts.

As noted by Mann (1982), estuarine seaweeds play a variety of functional roles in northern salt marshes, including primary production, provision of critical habitat for numerous organisms, and production of abundant organic matter via detrital cycles. Although these roles are generally understood, there are few detailed assessments of seaweed communities in Maine salt marshes, except for floristic descriptions of the York River Estuary (Mathieson et al. 1993) and inner riverine sections of the Great Bay Estuary System, including the Piscataqua and Salmon Falls Rivers (Mathieson and Hehre 1986; Mathieson and Penniman 1991).

The present study is intended to characterize the species composition and variability (i.e., spatially and temporally) of estuarine and nearshore open coastal seaweed populations between Cape Neddick, York, and Fort Foster, Kittery, Maine (Figures 1–3), including those of Brave Boat Harbor (hereafter designated as BBH). The latter site represents one of three major estuaries within this area, including, from north to south (Figures 1 and 2), the York River (Maine), BBH (Maine), and the Piscataqua River (Maine and New Hampshire). The Harbor is located in the townships of York and Kittery, Maine, and is partly owned by the National Wildlife Federation/U.S. Fish and Wildlife Service with-

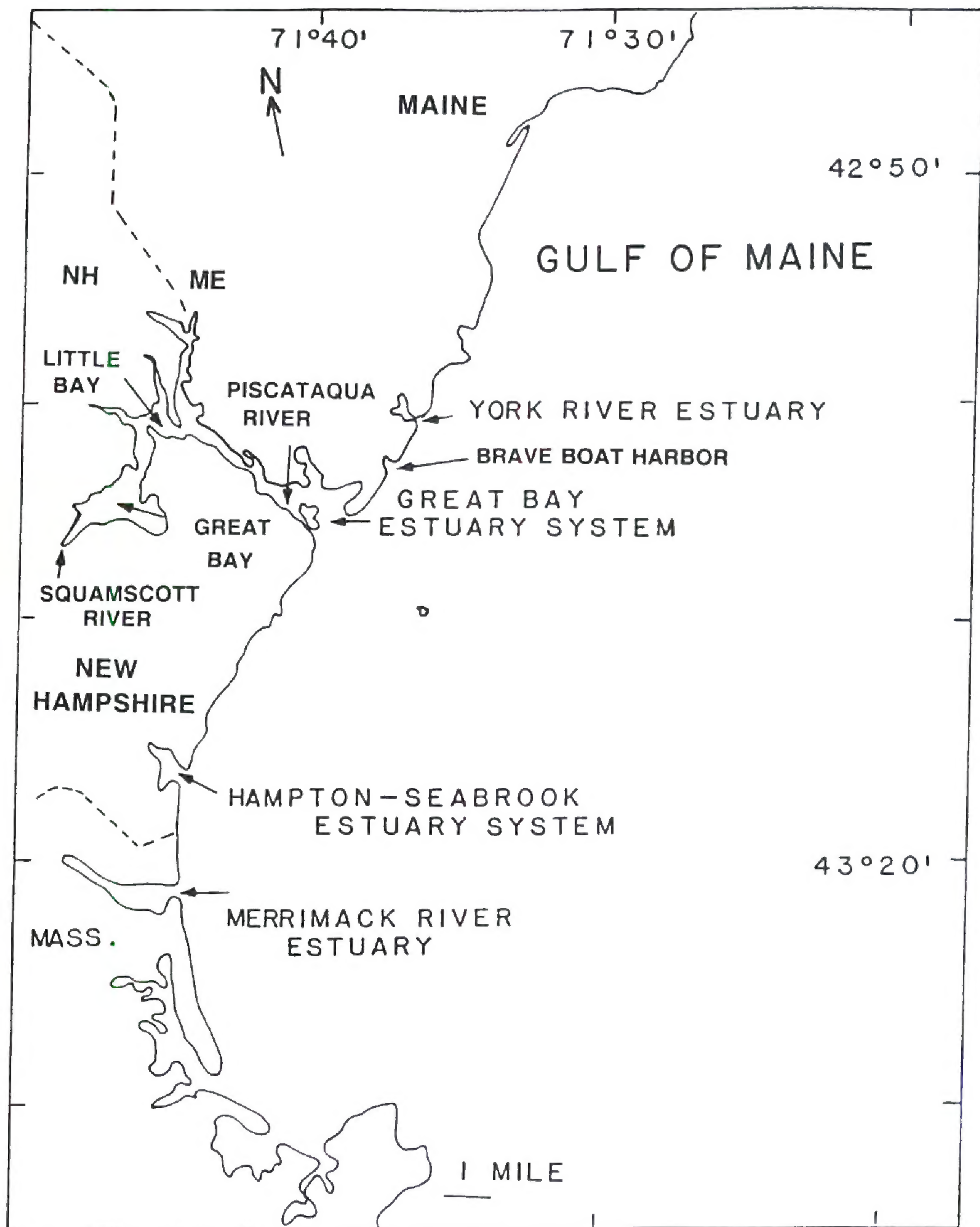


Figure 1. The coastline of northern New England between southern Maine and northern Massachusetts, showing diverse coastal and estuarine habitats.

in its Rachel Carson Wildlife Reserve (ca. 162 ha). It has a rich human history dating back to at least 1645, when sections of the marsh were allotted to residents for fodder and the rearing of cattle (archives, Kittery Historical Society). Records from the early 1700s detail the geography of BBH and its interrelationship with Gerrish Island, Cutts Island, Chauncey Creek, and the Kittery

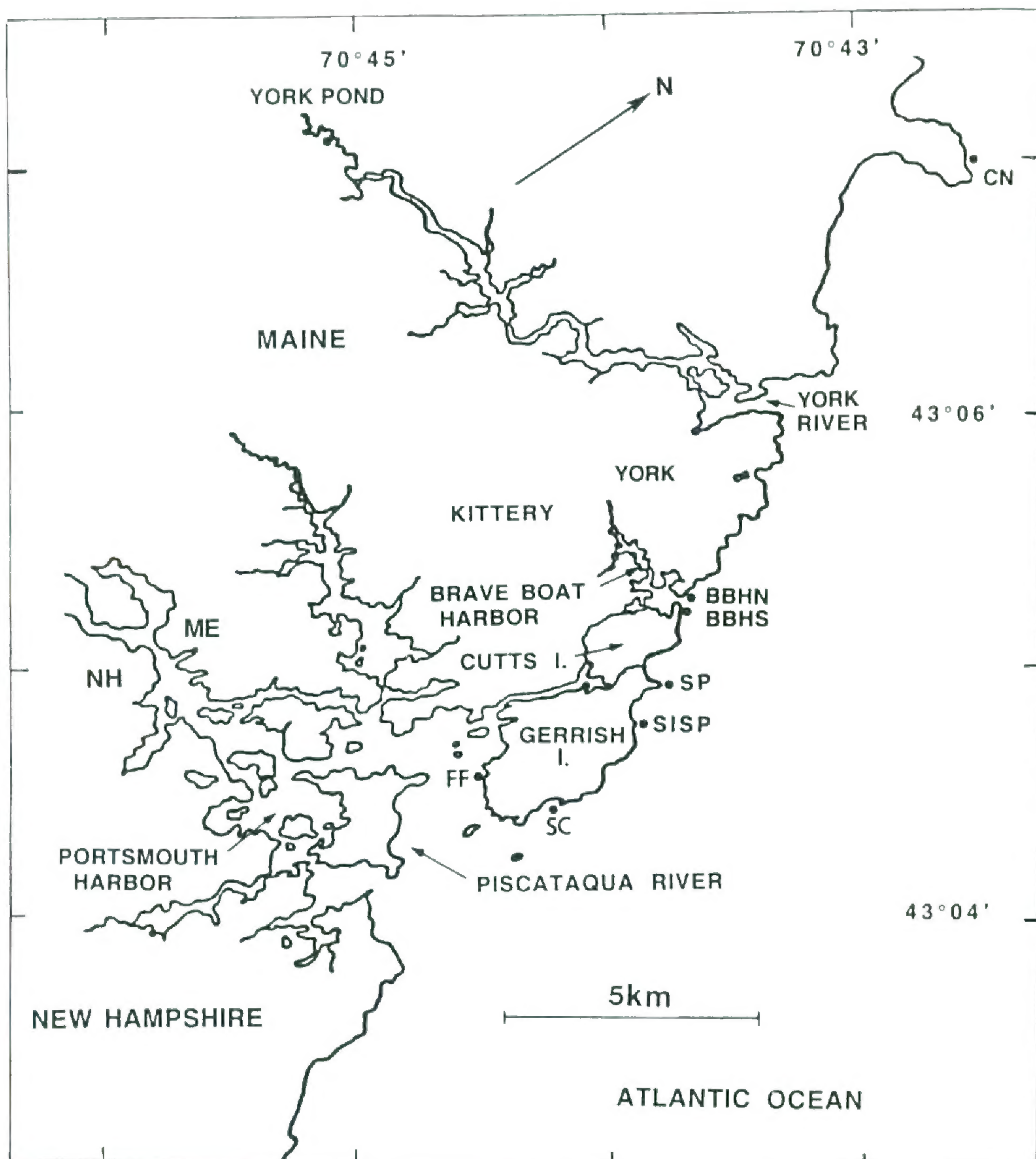


Figure 2. Southern Maine and New Hampshire coastlines, showing the location of coastal and estuarine habitats. See Appendix for abbreviations.

Point mainland (Figures 2 and 3). Both islands and Chauncey Creek are named for original settlers (cf. Samuel Drake's travel memoirs, archives, Kittery Historical Society).

The goals of our study were three-fold: (1) to compare the number and types of seaweeds from six coastal and estuarine habitats (Figures 2 and 3), including the BBH area of York/Kittery, Maine; (2) to provide a detailed floristic baseline that would aid in future conservation of these valuable habitats; (3) to compare distributional and floristic patterns in BBH with other estuaries within northern New England.

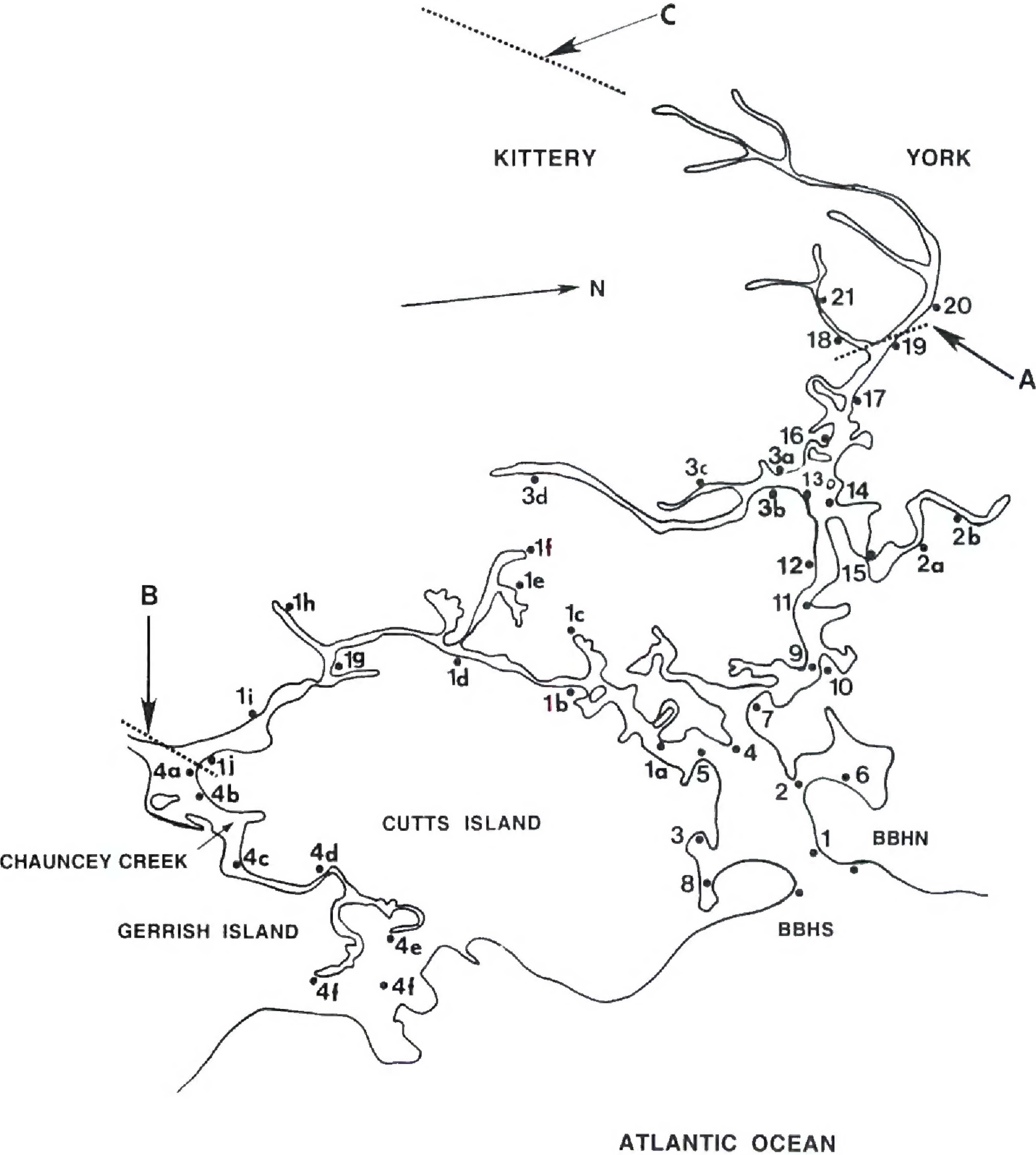


Figure 3. The twenty-one estuarine study sites along the main channel of Brave Boat Harbor (BBH), plus 23 other sites within four contiguous tidal tributaries. The dashed lines at letters “A” and “B” indicate the locations of road crossings and culvert at tributaries #1 and #4, respectively, while letter “C” designates the approximate delineation of town boundaries between York and Kitterry.

MATERIALS AND METHODS

Seasonal collections were made at 51 sites in southern Maine (Figures 2 and 3; Appendix): seven nearshore open coastal locations between Cape Neddick, York (43°09.93’N, 70°35.41’W), and Fort Foster, Kitterry, on the outermost Piscataqua River (43°04.0’N, 70°41.77’W); 21 estuarine sites along the main channel of BBH, York/Kitterry (43°06.0’N, 70°39.33’W); 23 additional

estuarine sites in four contiguous tidal tributaries of BBH and connected salt marshes (Figure 3). Descriptions of each site, including location, habitats, and substrata, are given in the Appendix. Periodic sampling of coastal populations was conducted between 1965–1985 (cf. Mathieson and Hehre 1986), while additional seasonal sampling of these and various BBH sites was done between 1997–1999.

Methods of collection and identification are similar to those of Mathieson et al. (1998), with seasonal collections of all conspicuous seaweeds from diverse intertidal (on foot) and shallow subtidal habitats (by SCUBA). Samples were returned (within one hour after being collected) to the Jackson Estuarine Laboratory, where they were identified and prepared as voucher specimens. The following taxonomic references were utilized: Adey and Adey 1973; Bird and McLachlan 1992; Blair 1983; Bliding 1963, 1968; Blomster et al. 1999; Burrows 1991; Dixon and Irvine 1977; Düwel and Wegeberg 1996; Farlow 1881; Fletcher 1987; Harper and Saunders, 2000; Hoek 1963, 1982; Irvine 1983; Irvine and Chamberlain 1994; Kingsbury 1969; Maggs and Hommersand 1993; Schneider and Searles 1991; Sears 1998; Silva et al. 1996; Taylor 1957; Villalard-Bohnsack 1995; Webber and Wilce 1971; Woelkerling 1973; Wynne and Heine 1992). The nomenclature employed primarily follows South and Tittley (1986), except for recent changes noted by Sears (1998) and Silva et al. (1996). Approximately 3500 voucher specimens documenting these studies have been deposited in the Albion R. Hodgdon Herbarium at the University of New Hampshire (NHA).

Several floristic comparisons have been made: (1) a compilation of species composition and number of taxa at each site; (2) an enumeration of percentage and mean number of total taxa for each of the six major coastal and estuarine habitats; (3) a summary of intraspecific patterns for total taxa in each habitat (e.g., the number of taxa at 21 BBH sites); (4) an assessment of number and percentage of shared taxa for each major habitat. Percent similarity values (C) were determined using Czekanowski's coefficient (Bray and Curtis 1957):

$$C = \frac{2W}{a + b}$$

where "a" is the number of taxa at the first site, "b" is the

number at the second site, and “W” is the number of taxa in common to both.

Longevity characteristics were enumerated according to the scheme outlined by Knight and Parke (1931), with taxa designated as annuals (aseasonal or seasonal), perennials, or pseudo-perennials, depending upon their life span, growth, and reproductive characteristics (Mathieson 1989). Delineations were based upon field studies throughout New England (Coleman and Mathieson 1975; Femino and Mathieson 1980; Hehre and Mathieson 1970; Hehre et al. 1970; Lamb and Zimmerman 1964; Mathieson 1979; Mathieson and Hehre 1982, 1983, 1986; Mathieson et al. 1993, 1996, 1998; Mathieson, Hehre and Reynolds 1981; Mathieson and Penniman 1986a, 1986b, 1991; Mathieson, Reynolds and Hehre 1981; Reynolds and Mathieson 1975; Sears and Wilce 1975; Stone et al. 1970; Webber and Wilce 1971). The number and percentage of annual and perennial taxa at each of the six major habitats were enumerated.

We compared the mean number of taxa per site in the BBH area and thirteen other estuaries between the York River in Maine and the Merrimack River in Massachusetts (Figure 1). The location, number of collecting sites, and extent of tidal limits for the BBH area are summarized in the Appendix. Similar data, based upon previous publications (Mathieson and Fralick 1972, 1973; Mathieson and Hehre 1986; Mathieson et al. 1993), is given below for the other estuarine habitats: York River, ME, 20 sites and 0–7.5 km; Piscataqua River, NH and ME, 59 sites and 0–19.4 km; Little Bay, NH, 21 sites and 13.8–19.8 km; Great Bay, NH, 16 sites and 20.6–25.1 km; Bellamy River, NH, 10 sites and 16.6–22.9 km; Cocheco River, NH, 17 sites and 20.2–25.3 km; Lamprey River, NH, 9 sites and 25.3–28.0 km; Oyster River, NH, 14 sites and 18.4–22.7 km; Salmon Falls River, NH and ME, 16 sites and 20–26.4 km; Squamscott River, NH, 16 sites and 25.9–36.3 km; Winnicut River, NH, 4 sites and 25.4–27.7 km; Hampton-Seabrook Estuary, NH, 49 sites and 0.6–5.9 km; the Merrimack River Estuary, MA, 19 sites and 0–13.7 km.

Seasonal measurements of surface water temperatures and salinities were recorded at seven sites in the main channel of BBH (Figure 3), extending from the mouth (site #1, 0.1 km inland) to tidal headwaters near Brave Boat Harbor Road (site #19, 1.6 km inland). This was accomplished using a hand-held thermometer and refractometer, with an accuracy of 0.1°C and 0.5‰, respec-

tively. Analogous sampling was done at seven sites along tributary #1, which delineates Cutts Island and has "coastal environments" at both ends (Figure 3; Appendix). Site #1a is located 0.53 and 4.2 km from the Harbor's mouth and open coast near Swards Cove, respectively, while #1j is 2.0 and 2.7 km from the same geographical locations. Most sampling was done at predicted low tides (Anonymous 1996), proceeding from outer to inner areas relative to the Harbor's mouth.

HABITAT DESCRIPTION AND ECOLOGY

The coastline between Cape Neddick, Maine, and Portsmouth Harbor, New Hampshire (Figure 2), has many geological and topographical features in common. These include the presence of scattered offshore islands (Boon Island and Isles of Shoals), broad arcuate bays, large rocky headlands, and scattered sandy barrier beaches in front of extensive salt marshes (cf. Mathieson and Hehre 1986). The terrain is relatively flat compared with coastal regions to the northeast. Bedrock is composed primarily of low-grade metasedimentary rock intruded by large plutons of granite and syenite (Belknap et al. 1987; Kelley 1987; Mathieson et al. 1991). Wave action on the nearshore open coast is variable, from exposed (Cape Neddick), to semi-exposed (Seapoint) and sheltered (Fort Foster). Substrata vary from massive rock outcrops to boulders, cobbles, and sand (cf. Appendix). Three major estuaries are located sequentially between Cape Neddick and Portsmouth Harbor (Figures 1 and 2): the York River Estuary, the BBH marsh complex (including the Cutts and Gerrish Island marshes), and the Piscataqua River. The York and Piscataqua Rivers are the largest estuarine habitats, extending 7.5 and 19.4 km inland, respectively; headwaters of the former are at York Pond (Mathieson et al. 1993); the latter merges into Little Bay, Great Bay, and the Squamscott River (Figure 1), extending 36.3 km inland (Mathieson and Hehre 1986). The main tidal channel at BBH is about 1.9 km in length; Cutts and Gerrish Island marshes are inner tidal tributaries and extend 0.39–4.2 and 2.4–4.2 km inland, respectively (cf. Appendix).

Brave Boat Harbor (about 2.7 km²) is located behind a sand and cobble barrier beach near Seapoint (Figures 2 and 3; Appendix). The sand body inside the mouth of the Harbor resembles a flood tidal delta (Boothroyd 1978). However, the currents are

weaker than those of classical mesotidal estuaries like the Parker River and Essex Bay in Massachusetts and provide a somewhat different configuration (Franz Anderson, pers. comm.). Tides near the mouth of BBH are uniformly semi-diurnal, with an average amplitude of about 2.6 m (Anonymous 1996). Currents and periodic inundations cause variable salinities from the mouth to the tidal headwaters at Brave Boat Harbor Road (see below).

The main channel of BBH is divided by the York and Kittery town line (Figure 3). Although it is sparsely populated and devoid of industry, shellfish harvesting is restricted to the outer Harbor due to contamination by fecal coliform bacteria. Tributaries #1 and #4 show some signs of eutrophication, presumably due to septic discharge.

The BBH salt marshes were probably formed about 10,000 years before present (YBP), following the last retreat of the Wisconsin ice sheet and subsequent stabilization of sea levels (Belknap et al. 1987; Jacobson and Jacobson 1989; Jacobson et al. 1987). Most tidal marshes in the Gulf of Maine flourished during this time, filling upper bays behind coastal sand barriers and diminishing their tidal channels into smaller creeks. Like other salt marshes between southern Maine and Massachusetts, BBH receives an abundance of fresh water (Jacobson et al. 1987). However, it is a more sandy and erosive environment than the York and Piscataqua Rivers or the Cutts and Gerrish Islands marshes (Mathieson and Hehre 1986; Mathieson et al. 1993), and it is more analogous geologically to New Hampshire's Hampton-Seabrook Estuary (Mathieson and Fralick 1972) and the Parker River area of Massachusetts (Boothroyd 1978). There is extensive erosion of BBH's outer marsh (Figure 4), possibly reflecting strong tidal currents, rising sea levels (Stevenson et al. 1986), and reduced sediments due to expansion of New England forests and increased soil conservation measures over the past 100 years. Many deep ponds and potholes occur in the outer marsh (see below), probably caused by ice rafting, surface collapse from undermining of the sand layer, and dieback of marsh grass because of wrack deposition. Thus, the outer marsh shows a patchy physiography, with extensive dissection and superficial channels.

The entrance to BBH's main channel (sites BBHN and BBHS; Figures 2 and 3) is dominated by boulders and cobbles (cf. Appendix), which were probably deposited after the retreat of the Laurentide Glacier about 50,000 YBP (Kelley 1987). Just inside

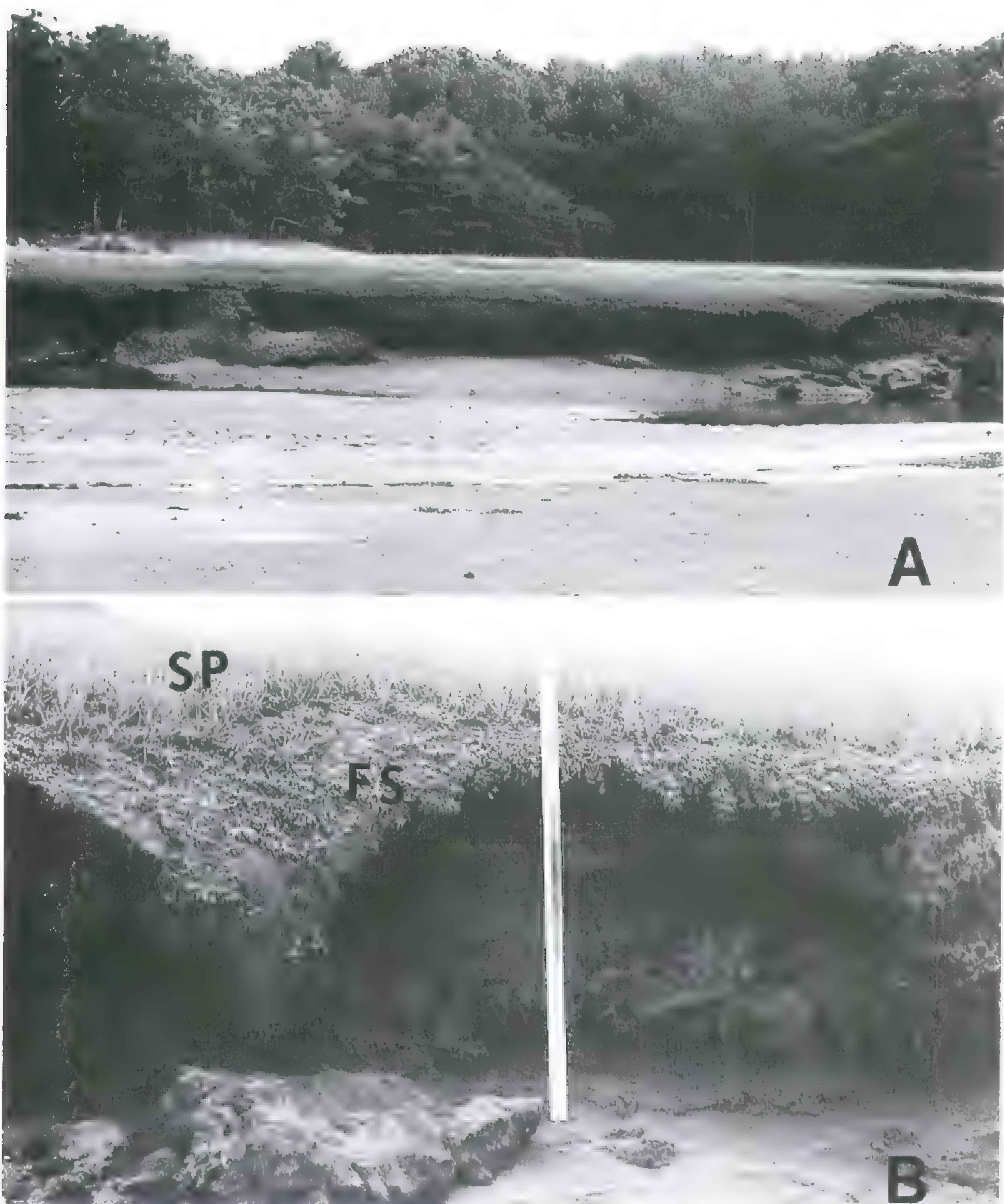


Figure 4. Photographs of the main tidal channel of Brave Boat Harbor showing (A) the broad, sandy mouth and (B) nearby eroded bluffs (1.5–3 m high) with high marsh vegetation consisting of *Spartina patens* (SP) and an understory of the dwarf muscoides-like *Fucus*. *Fucus spiralis* (FS) is attached to the sediment below the high marsh while *Pilayella littoralis* occurs as strands hanging from the cliff.

the Harbor's mouth, the shoreline is sandy and resembles a flood tidal delta (Boothroyd 1978). The exposed nature of this area is demonstrated by several features: (1) surface ripples on the sand caused by tidal currents; (2) absence of a low marsh with *Spartina alterniflora* Loisel.; (3) extensive erosion and slumping of the

marsh (Figure 4A); and (4) the presence of 2 to 3 m high cliffs extending from the high marsh to bare sediment (Figure 4B). Inland, the tidal channel is sheltered, sediments are dominated by fine sand, rocky outcrops are limited, and high and low marshes occur (cf. Appendix). High marsh communities have abundant *S. patens* (Aiton) Muhl., scattered *Festuca rubra* L., *Juncus gerardii* Loisel., *Limonium nashii* Small, *Salicornia europaea* L., *Suaeda maritima* (L.) Dumort., and *Triglochin maritima* L., plus a turf-forming moss or “muscoide-like” *Fucus* (see below). *Spartina alterniflora* and the entangled/embedded understory fucoids *Ascophyllum nodosum* ecad *scorpioides* and *Fucus vesiculosus* ecad *volubilis* dominate low marshes within the middle and inner Harbor.

The first of four contiguous tidal tributaries is located on the Kittery side of the outer Harbor; it delineates Cutts Island and is exposed to “coastal” waters at both ends (Figure 3). The entrance to the first tributary (#1a) is located about 0.39 and 4.2 km inland from the open coast via the Harbor mouth and Sowards Cove, respectively (Appendix). The second tributary (#2) is located in York and extends about 1.3 to 1.7 km inland, while tributary #3 is in Kittery and extends 1.2 to 1.8 km inland. The fourth tributary, Chauncey Creek (Kittery), separates Gerrish and Cutts Islands from the mainland and from each other; it extends 2.4 to 4.2 km inland and its vegetation is similar to the inner reaches of BBH (cf. Appendix).

Water temperatures during six seasonal samplings were spatially similar throughout the Harbor, except at the two innermost sites during June and August (Figure 5A). The latter differed from open coastal sites, with temperatures of 16–18°C versus 18–23°C in June and 21–22°C versus 18–19°C in August. A strong seasonal change is evident throughout the Harbor, from 22°C in June to less than 0°C in February. Salinities near the mouth vary from 32‰ in February to 18‰ in June, the latter following a period of heavy rainfall (Figure 5B). With the exceptions of August and October, salinities decreased to 0‰ near the inner tidal dam. The stable high salinities (32‰) of August were associated with a prolonged period of hot, dry weather and limited fresh water discharge.

Figure 6 shows the effects of a “divide” in tributary #1. Salinities for February and October, 1998 were low (11–13‰) at 1.8 and 1.6 km inland from the mouth of BBH and higher (ca.

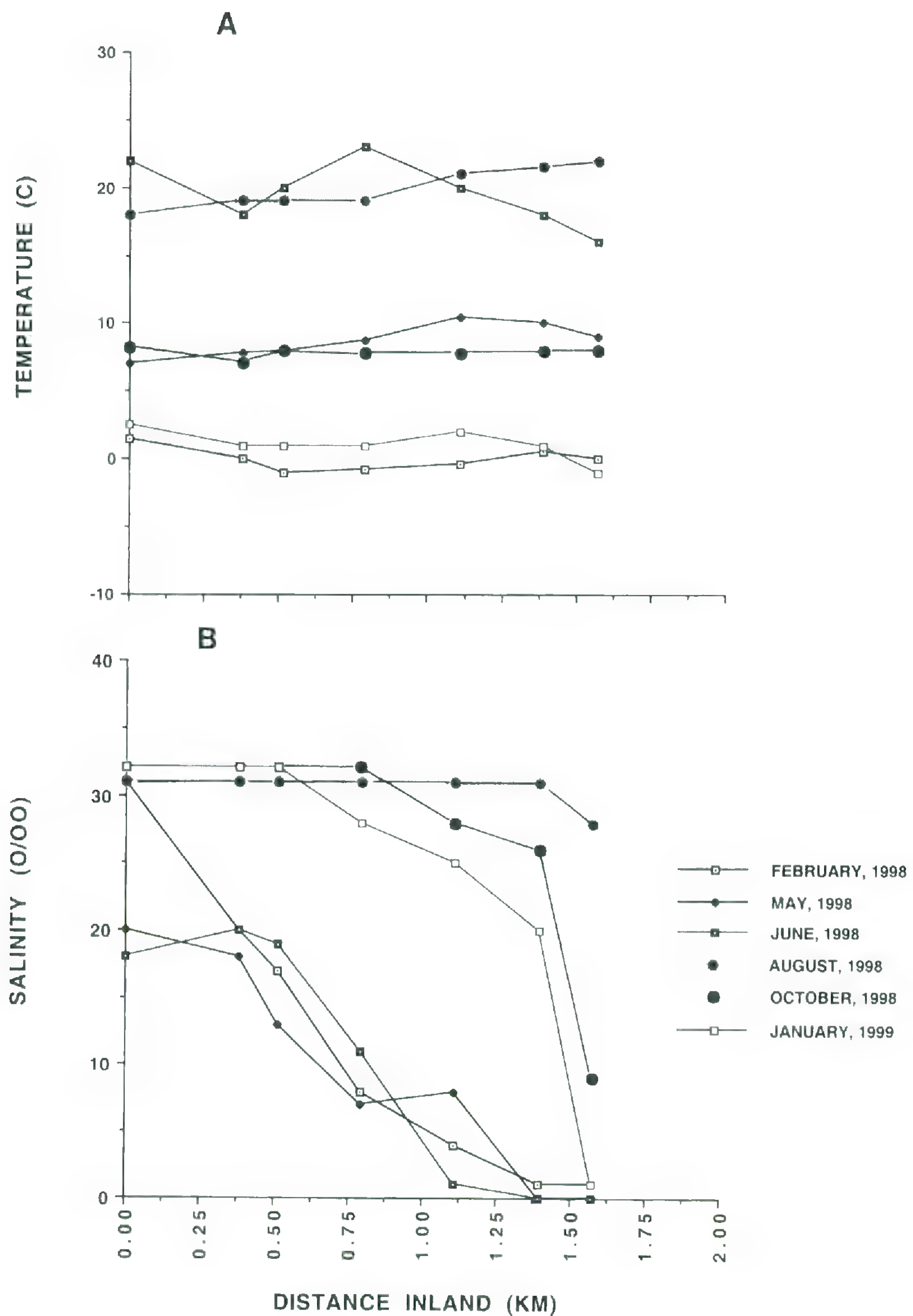


Figure 5. Surface water temperatures (A) and salinities (B) within Brave Boat Harbor during six seasonal sampling periods between February, 1998 and January, 1999. The site locations are plotted in km inland from the open mouth of the Harbor.

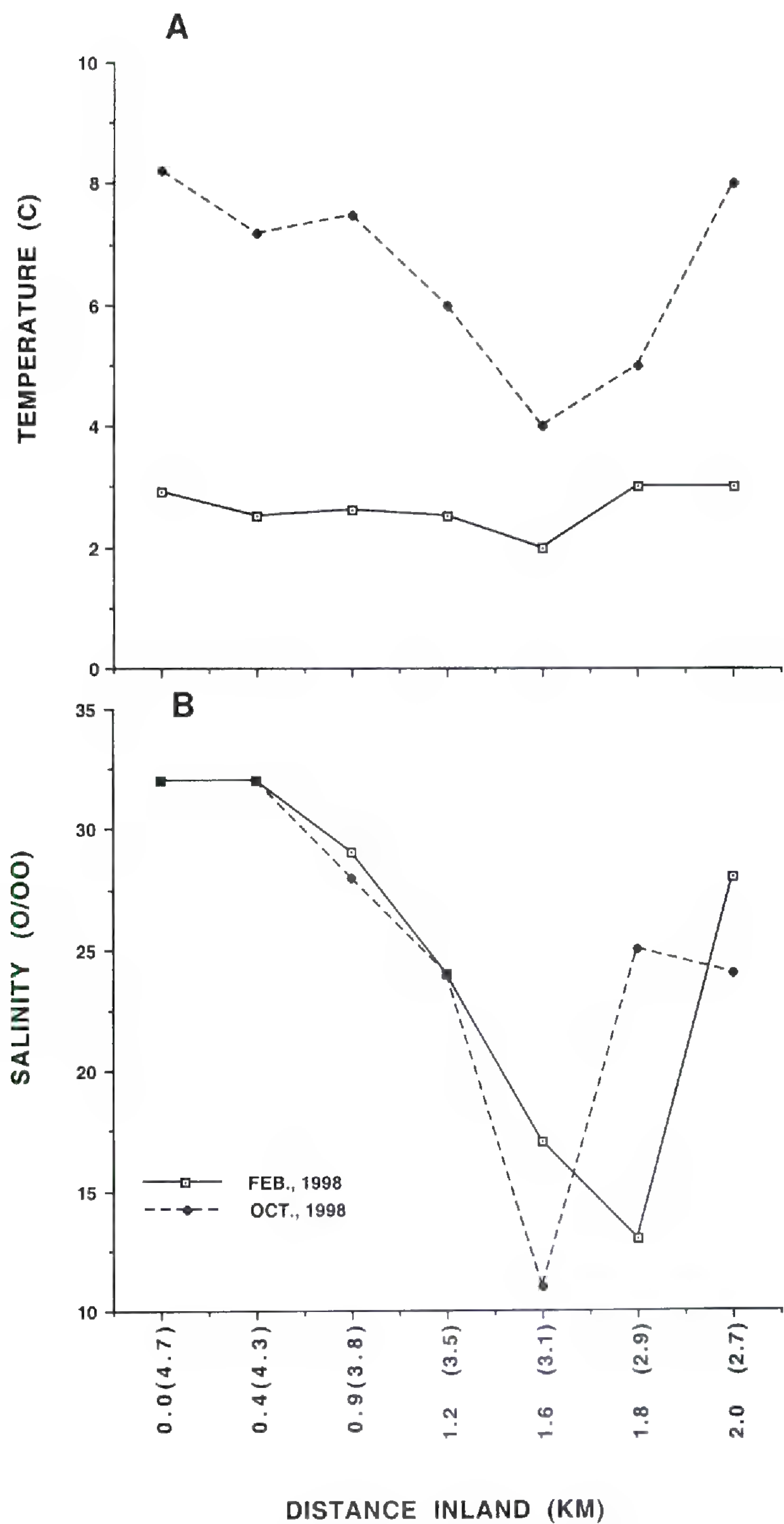


Figure 6. Surface water temperatures (A) and salinities (B) within tributary #1 that delineates Cutts Island from the main tidal channel of Brave Boat Harbor. Measurements made during February and October, 1998 show the effects of a “divide” and localized fresh water discharge. Distances (in km) represent site locations inland from the Harbor’s mouth and Swards Cove, respectively.

32‰) at both ends. Localized fresh water discharge and an enhanced elevation (a “divide”) near the tributary’s center cause tides to ebb in both directions. Surface water temperatures were uniform in February (2.5–3.0°C) but more spatially variable in October (4.0–8.2°C), the lowest values occurring at 1.6 km.

Ice is common during December to March within inner parts of BBH. During early winter skim ice may form on ebb tides, often disappearing on the subsequent flood tide. Over time, an “ice foot,” or belt of fast-ice (Grøen 1967), freezes to the shore and does not float upwards at high tides. Typically, ice formation is greater in shallow ponds than in narrow tidal channels with stronger currents. Scouring effects are evident on rocks, pier pilings, and other substrata. Large sections of marshy shoreline may be torn loose (rafted) during spring thaws and transported to new sites (cf. Hardwick-Witman 1985, 1986; Mathieson et al. 1982).

RESULTS

Species composition and distributional patterns. A total of 148 seaweed taxa (39 Chlorophyceae, 48 Phaeophyceae, and 61 Rhodophyceae) was recorded from 51 study sites (Table 1; Figure 7). The benthic colonial diatom *Berkeleya rutilans* (Bacillariophyceae) occurred at 15 sites. Six new or uncommon taxa were recorded from BBH, including *Codium fragile* subsp. *tomentosoides*, *Urospora curvata*, *Melanosiphon intestinalis*, *Fucus vesiculosus* ecad *volubilis*, *F. spiralis* ecad *lutarius*, and the “muscoide-like” *Fucus*. The introduced siphonaceous green alga *Codium* grew abundantly in ponds near the mouth of BBH, and it was previously unknown from salt marsh habitats in Maine. The microscopic green alga *U. curvata* occurred as an epiphyte on fucoids, with its occurrence at Seapoint and BBH representing the first records of this taxon from nearshore areas in Maine. The tubular and opportunistic brown alga *M. intestinalis* was common on eroded and muddy channel embankments, while it was absent from adjacent nearshore open coastal habitats. Three detached fucoid ecads occurred as entangled or partially embedded fragments, with *Ascophyllum nodosum* ecad *scorpioides* occurring at 67% of the sites, *F. vesiculosus* ecad *volubilis* at 49%, and *F. spiralis* ecad *lutarius* at 29%. In distinguishing *F. spiralis* ecad *lutarius* and *F. vesiculosus* ecad *volubilis*, the former is a relatively narrow, proliferous, and evesiculate plant, while the latter

is a broader, proliferous, and more spiraled plant that often bears vesicles (Baker and Bohling 1916; Chapman 1939). The “muscoïdes-like” *Fucus* (previously designated as *Fucus cottonii* M. J. Wynne et Magne, *F. muscoïdes*, *F. vesiculosus* variety *muscoïdes*, and *F. vesiculosus* ecad *muscoïdes*) is a minute turf-like plant that forms “lawns” in upper sandy salt marshes (Norton and Mathieson 1983). It occurred at 31% of the sites and was newly recorded from the northwest Atlantic.

Seaweed populations from the 51 study sites exhibited three major distributional patterns (Table 1; Figure 7): coastal (C), restricted to the nearshore open coast (29 red, 22 brown, and 9 green algae; 41%); coastal-estuarine (C-E), occurring in coastal and estuarine habitats (30 red, 19 brown, and 26 green algae; 51%); and estuarine (E), restricted to estuarine habitats (2 red, 7 brown, and 4 green algae; 8%).

Thirty-four of the 60 coastal taxa (57%) occurred at two or more coastal sites (including Fort Foster); the remaining 26 (43%) were restricted to a single site (Table 1). Some localized coastal taxa included *Chaetomorpha brachygona*, *Chorda filum*, *Petalonia zosterifolia*, *Devaleraea ramentacea*, and *Plumaria plumosa*.

Coastal-estuarine species also exhibited varying distributional patterns (Table 1). *Ascophyllum nodosum*, *Pilayella littoralis*, *Rhizoclonium riparium*, *Ulothrix speciosa*, and *Blidingia minima* occurred at 63–71% of the sites, while nine others, including *Hildenbrandia rubra* and *Chondrus crispus*, occurred at more than 41%. Nineteen C-E taxa were restricted to the five outermost sites and included *Bryopsis plumosa*, *Desmarestia aculeata*, *Corallina officinalis*, and *Ptilota serrata*. Twenty-seven C-E taxa had restricted (less than 20%) and patchy estuarine distributions, including *Codium fragile* subsp. *tomentosoides*, *Spongomorpha arcta*, *Dictyosiphon foeniculaceus*, *Laminaria saccharina*, and *Ceramium rubrum*.

Seven of the thirteen estuarine taxa (54%) were uncommon, being restricted to 1–2 sites (*Acrochaete wittrockii*, *Capsosiphon fulvescens*, *Ulothrix flacca*, *Punctaria tenuissima*, *Stictyosiphon soriferus*, *Polysiphonia nigra*, and *Porphyra purpurea*). By contrast, *Ascophyllum nodosum* ecad *scorpioides* and *Fucus vesiculosus* ecad *volubilis* occurred at 63% of the sites.

Frequency distribution patterns of the 148 seaweed taxa are shown in Table 1 and Figure 8. Twenty-nine taxa (4 green, 10 brown, and 15 red algae) were rare, being restricted to one site

Table 1. Summary of seaweed taxa at 51 study sites within southern Maine, including the individual site records, percent occurrence, coastal versus estuarine distributional patterns, and longevity features for each taxon; () = % occurrence value, C = coastal only, C-E = coastal and estuarine, E = estuarine only, Ann. = annual, AAnn. = aseasonal annual, Per. = perennial, PPer. = pseudoperennial, “ ” = potential life history stage. See Appendix for habitat descriptions and abbreviations.

	Collection Sites, % Occurrence, and Longevity
BACILLARIOPHYCEAE	
<i>Berkeleya rutilans</i> (Trentopohl) Grönow	III, IV, VII, 3-5, 7, 9, 12, 14, 17, 1d, 1g, 1j, 3a (29%), C-E: Ann.
TOTAL DIATOM TAXA = 1	
CHLOROPHYCEAE	
<i>Acrochaete wittrockii</i> (Wille) R. Nielsen	7 (2%), E: Ann.
<i>Blidingia minima</i> (Nägeli ex Kützing) Kylin	I, III, IV, VI, VII, 1-5, 7-9, 12-21, 1b, 1d, 1g, 1i, 1j, 3a-3d, 4b, 4c, 4e, 4g (71%), C-E: Ann.
<i>Bryopsis plumosa</i> (Hudson) C. Agardh	II, 4 (4%), C-E: Ann.
<i>Capsosiphon fulvescens</i> (C. Agardh) Setchell et Gardner	1 (2%), E: Ann.
<i>Chaetomorpha aerea</i> (Dillwyn) Kützing	IV, VI (4%), C: Per.
<i>Chaetomorpha brachygona</i> Harvey	IV (2%), C: Ann. (?)
<i>Chaetomorpha linum</i> (O. F. Müller) Kützing	I, IV, 4, 9, 16, 1f, 1i, 1j, 4b (18%), C-E: Per.
<i>Chaetomorpha melagonium</i> (F. Weber et D. Mohr) Kützing	I, IV, VII (6%), C: Per.
<i>Chaetomorpha picquotiana</i> Montagne ex Kützing	I-IV, VII, 1, 4, 7, 9 (18%), C-E: Per.
“ <i>Chlorochytrium inclusum</i> Kjellman”	IV, 1 (4%), C-E: Ann.
<i>Cladophora albida</i> (Nees) Kützing	I, IV (4%), C: AAnn.
<i>Cladophora sericea</i> (Hudson) Kützing	I, III, IV, VII, 4, 5, 7, 8, 10, 15, 16, 1j (24%), C-E: AAnn. or PPer.
“ <i>Codiolum pusillum</i> (Lyngbye) Kjellman”	IV, 19 (4%), C-E: Ann.
<i>Codium fragile</i> (Suringar) Hariot	
subsp. <i>tomentosoides</i> (van Goor) P. C. Silva	I, III-V, VII, 4, 5, 7, 8 (18%), C-E: Per.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
<i>Enteromorpha flexuosa</i> (Wulfen <i>ex</i> Roth) J. Agardh	
subsp. <i>paradoxa</i> (C. Agardh) Bliding	I, IV, 9 (6%), C–E: Ann.
<i>Enteromorpha intestinalis</i> (L.) Ness	
subsp. <i>intestinalis</i>	I, IV, V, VII, 1, 3–5, 9, 12, 14, 16–19, 21, 1j, 3a–3c (39%), C–E: Ann.
<i>Enteromorpha intestinalis</i> (L.) Ness	
subsp. <i>compressa</i> Collins	IV, VII, 3, 4, 9 (10%), C–E: Ann.
<i>Enteromorpha linza</i> (L.) J. Agardh	I, IV, 1j (6%), C–E: Ann.
<i>Enteromorpha muscoides</i> (Clemente <i>et</i> Rubio) Cremades	I, IV, 3, 4, 8, 9, 14, 16, 18, 1a–1c, 1e, 2b, 3a–3c, 4a (35%), C–E: Ann.
<i>Enteromorpha prolifera</i> (O. F. Müller) J. Agardh	I, IV, 9, 16, 4c (10%), C–E: Ann.
<i>Microspora pachyderma</i> (Wille) Lagerheim	IV, 1, 2, 4, 5, 7–10, 14, 15, 17–20, 1b, 2b, 3c, 3d, 4c, 4g (41%), C–E: Ann.
<i>Monostroma grevillei</i> (Thuret) Wittrock	I, IV–VII, 4, 5, 14, 16, 1d, 1g, 1i, 1j, 4c (27%), C–E: Ann.
<i>Monostroma oxyspermum</i> (Kützinger) Doty	3–5, 7, 9, 10, 15, 18, 1d, 1f, 1g, 1i, 3a–3d, 4a–4d (39%), C– E: Ann.
<i>Percursaria percursa</i> (C. Agardh) Rosenvinge	1–5, 7, 8 (14%), E: Ann.
<i>Prasiola stipitata</i> Suhr <i>ex</i> Jessen	I (2%), C: Ann.
<i>Pringsheimiella scutata</i> (Reinke) Höhnelt <i>ex</i> Marchewianka	IV, 1, 5 (6%), C–E: Ann.
<i>Protomonostroma undulatum</i> (Wittrock) K. L. Vinogradova	
f. <i>pulchrum</i> (Farlow) M. J. Wynne	I, III, IV (6%), C: Ann.
<i>Pseudendoclonium submarinum</i> Wille	IV, 1, 6, 8, 9, 3c (12%), C–E: AAnn.
<i>Rhizoclonium riparium</i> (Roth) Harvey	I, IV, 1–5, 8–10, 12, 14–18, 1a–1c, 1e–1g, 1i, 2j, 2a, 3a–3d, 4a–4d (65%), C–E: Ann.
<i>Rhizoclonium tortuosum</i> (Dillwyn) Kützinger	I, III, IV, VII, 1, 4, 9 (14%), C–E: AAnn.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
<i>Spongomorpha arcta</i> (Dillwyn) Kützing	I, IV, VII, 4, 5, 16 (12%), C–E: Ann.
<i>Spongomorpha spinescens</i> Kützing	I, IV, VII (6%), C: Ann.
<i>Ulothrix flacca</i> (Dillwyn) Thuret in Le Jolis	2, 20 (4%), E: Ann.
<i>Ulothrix speciosa</i> (Carmichael ex Harvey in Hooker) Kützing	IV, V, VII, 2–5, 7–9, 12–21, 1b, 1d, 1f–1j, 3b–3d, 4b–4e, 4g (69%), C–E: Ann.
<i>Ulva lactuca</i> L.	I, III, IV, VII, 1, 3, 4, 8, 9, 14, 19, 1d, 1j, 4b, 4c, 4e, 4g (33%), C–E: AAnn. or PPer.
<i>Ulvaria obscura</i> (Kützing) Gayral	I, IV, 14 (6%), C–E: Ann.
<i>Urospora curvata</i> (Printz) Kornmann et Sahling	IV, 4, 16 (6%), C–E: Ann.
<i>Urospora penicilliformis</i> (Roth) Areschoug	I, IV–VII, 1, 19, 4c (16%), C–E: Ann.
<i>Urospora wormskjoldii</i> (Mertens in Hornemann) Rosenvinge	I (2%), C: Ann.
TOTAL GREEN ALGAL TAXA = 39	
PHAEOPHYCEAE	
<i>Agarum clathratum</i> Dumortier	I, II, IV–VII (12%), C: Per.
<i>Alaria esculenta</i> (L.) Greville	I, IV, VII (6%), C: Per.
<i>Ascocyclus distromaticus</i> W. R. Taylor	I (2%), C: Ann.
<i>Ascophyllum nodosum</i> (L.) Le Jolis	I–VII, 1, 3–5, 7–9, 11, 13, 14, 16, 17, 1a, 1c, 1d, 1f, 1g, 1i, 1j, 2b, 3d, 4a–4d (63%), C–E: Per.
<i>Ascophyllum nodosum</i> (L.) Le Jolis	
<i>ecad scorpioides</i> (Hornemann) Reinke	1–18, 1a–1d, 1f, 1g, 1i, 1j, 2a, 3a–3d, 4b–4d (67%), E: Per.
<i>Chorda filum</i> (L.) Stackhouse	I (2%), C: Ann.
<i>Chorda tomentosa</i> Lyngbye	I (2%), C: Ann.
<i>Chordaria flagelliformis</i> (O. F. Müller) C. Agardh	I, IV (4%), C: Ann.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
<i>Desmarestia aculeata</i> (L.) J. V. Lamouroux	I–VII, 4, 5 (18%), C–E: Per.
<i>Desmarestia viridis</i> (O. F. Müller) J. V. Lamouroux	I, IV, V, 5 (8%), C–E: Ann.
<i>Dictyosiphon foeniculaceus</i> (Hudson) Greville	I, IV, 9 (6%), C–E: Ann.
<i>Ectocarpus fasciculatus</i> Harvey	IV, 5, 17 (6%), C–E: Ann.
<i>Ectocarpus siliculosus</i> (Dillwyn) Lyngbye	I, IV, VI, 1, 4, 5, 7, 16 (16%), C–E: Ann.
<i>Elachista fucicola</i> (Vellay) Areschoug	I, IV, V, VII, 2–5, 8, 9, 1j, 3d (24%), C–E: Per.
<i>Eudesme virescens</i> (Carmichael ex Berkeley) J. Agardh	I, IV, (4%), C: Ann.
<i>Fucus distichus</i> L. emend Powell	
subsp. <i>distichus</i>	I, III, IV (6%), C: Per.
<i>Fucus distichus</i> L. emend Powell	
subsp. <i>edentatus</i> (de la Pylaie) Powell	I, IV (4%), C: Per.
<i>Fucus distichus</i> L. emend Powell	
subsp. <i>evanescens</i> (C. Agardh) Powell	I, III–VII, 1 (14%), C–E: Per.
<i>Fucus</i> “muscoides-like” form	2–12, 14, 17, 1b, 3a, 3c (31%), E: Per.
<i>Fucus spiralis</i> L.	I–VI, 1–12, 14, 16, 17, 1b, 1d, 1f, 1g, 3d (51%), C–E: Per.
<i>Fucus spiralis</i> L.	
ecad <i>lutarius</i> (Kützinger) Sauvageau	2–10, 12, 14, 1i, 1j, 3a, 4b (29%), E: Per.
<i>Fucus vesiculosus</i> L.	I–VII, 2–4, 8, 9, 13, 15, 1d, 1f, 1g, 1i, 1j, 3c, 3d, 4a–4d (49%), C–E: Per.
<i>Fucus vesiculosus</i> L.	
ecad <i>volubilis</i> (Hudson) Turner	1–5, 7–17, 1a–1d, 1g, 1i, 1j, 2a, 3a–3d, 4b–4d, 4g (63%), E: Per.
<i>Laminaria digitata</i> (Hudson) J. V. Lamouroux	I, II, IV, V, VII (10%), C: Per.
<i>Laminaria saccharina</i> (Hudson) J. V. Lamouroux	I–VII, 4, 1j (18%), C–E: Per.
<i>Laminariocolax tomentosoides</i> (Farlow) Kylin	I (2%), C: Ann. (?)
<i>Leathesia difformis</i> (L.) Areschoug	I (2%), C: Ann.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
<i>Melanosiphon intestinalis</i> (D. A. Saunders) M. J. Wynne	1–5, 7, 8, 10, 14, 17, 1g, 3a, 3c (25%), E: Ann.
<i>Mikrosyphar porphyrae</i> Kuckuck	I, IV (4%), C: Ann.
<i>Myrionema corunnae</i> Sauvageau	I, IV, 1j (6%), C–E: Ann.
<i>Petalonia fascia</i> (O. F. Müller) Kuntze	I–VII, 1–5, 7–9, 13, 14, 16, 17, 1d, 1g, 1i, 1j, 3c, 4b–4d (53%), C–E: Ann.
<i>Petalonia zosterifolia</i> (Reinke) Kuntze	IV (2%), C: Ann.
<i>Petroderma maculiforme</i> (Wollny) Kuckuck	IV, 19, 1g (6%), C–E: Per.
<i>Pilayella littoralis</i> (L.) Kjellman	I, II, IV, V, VII, 1, 3–5, 9, 10, 12–19, 1b, 1d–1g, 1i, 1j, 3a–3d, 4b, 4d, 4e (65%), C–E: Ann.
<i>Protectocarpus speciosus</i> (Børgesen) Kuckuck	IV (2%), C: Ann.
<i>Pseudolithoderma extensum</i> (Crouan frat.) S. Lund	IV, 14 (4%), C–E: Per.
<i>Punctaria plantaginea</i> (Roth) Greville	
var. <i>plantaginea</i>	I (2%), C: Ann.
<i>Punctaria tenuissima</i> (C. Agardh) Greville	5 (2%), E: Ann.
“ <i>Ralfsia clavata</i> (Harvey in Hooker) Crouan frat.”	II–VI, 1, 4–6, 8, 14, 16, 17, 1a, 1b, 1i, 4b, 4d (33%), C–E: Per.
<i>Ralfsia verrucosa</i> (Areschoug) J. Agardh	I, III, IV, VI, VII, 1, 3–8, 13, 14, 16, 17, 19, 1c, 1g, 1i, 1j, 3c, 3d, 4a–4c (51%), C–E: Per.
<i>Saccorhiza dermatodea</i> (de La Pylaie) Areschoug	I, IV, VII (6%), C: Ann.
<i>Scytosiphon lomentaria</i> (Lyngbye) Link	
var. <i>lomentaria</i>	I–VII, 1, 3–5, 7–9, 12, 14–17, 1d, 1f, 1g, 1i, 1j, 3c, 3d, 4b, 4d (55%), C–E: Ann.
<i>Sphacelaria arctica</i> Harvey	I, IV (4%), C: Per.
<i>Sphacelaria cirrosa</i> (Roth) C. Agardh	I, III, IV, VI, VII, 3–5, 7–9, 1j (24%), C–E: Per.
<i>Sphacelaria plumosa</i> Lyngbye	IV (2%), C: Per.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
<i>Sphacelaria radicans</i> (Dillwyn) C. Agardh	IV (2%), C: Per.
<i>Spongonema tomentosum</i> (Hudson) Kützing	I, IV (4%), C: Per. (?)
<i>Stictyosiphon soriferus</i> (Reinke) Rosenvinge	5 (2%), E: Ann.
TOTAL BROWN ALGAL TAXA = 48	
RHODOPHYCEAE	
<i>Ahnfeltia plicata</i> (Hudson) Fries	I, III, IV, VI, VII, 1, 3–5 (18%), C–E: Per.
<i>Antithamnionella floccosa</i> (O. F. Müller) Whittick	I, IV (4%), C: AAnn.
<i>Audouinella alariae</i> (H. Jónsson) Woelkerling	I (2%), C: Ann.
<i>Audouinella polyides</i> (Rosenvinge) Garbary	IV (2%), C: Ann.
<i>Audouinella purpurea</i> (Lightfoot) Woelkerling	I, III, IV, VII (8%), C: Per.
<i>Audouinella secundata</i> (Lyngbye) P. S. Dixon	I, II, IV, 1, 1j (10%), C–E: Ann.
<i>Bangia atropurpurea</i> (Roth) C. Agardh	I, IV–VII, 5, 19 (14%), C–E: Ann.
<i>Bonnemaisonia hamifera</i> Hariot	I, III, IV (6%), C: Per.
<i>Callithamnion tetragonum</i> (Withering) S. F. Gray	IV, 1j (4%), C–E: Per.
<i>Callocolax neglectus</i> F. Schmitz ex Batters	I, IV, 5 (6%), C–E: Per.
<i>Ceramium rubrum</i> (Hudson) C. Agardh	I, III, IV, VI, VII, 4, 5, 7 (16%), C–E: Per.
<i>Ceratocolax hartzii</i> Rosenvinge	IV (2%), C: Per.
<i>Chondrus crispus</i> Stackhouse	I–IV, VI, VII, 2, 4, 5, 7, 8, 13, 14, 16, 17, 1d, 1g, 1i, 1j, 3c, 3d, 4d (43%), C–E: Per.
<i>Choreocolax polysiphoniae</i> Reinsch	I, IV (4%), C: Per.
<i>Clathromorphum circumscriptum</i> (Strömfelt) Foslie	I–VII, 4, 16 (18%), C–E: Per.
<i>Coccotylus truncatus</i> (Pallas) M. J. Wynne et Heine	I, III, IV, VI, VII, 4 (12%), C–E: Per.
<i>Corallina officinalis</i> L.	I–VII, 1 (16%), C–E: Per.
<i>Cystoclonium purpureum</i> (Hudson) Batters	I, III, IV, VI, VII, 4 (12%), C–E: Per.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
<i>Devaleraea ramentacea</i> (L.) Guiry	I (2%), C: Per.
<i>Dumontia contorta</i> (S. G. Gmelin) Ruprecht	I, II, IV–VII, 2, 4, 5, 7–9, 13, 14, 16, 17, 1d, 1g, 1i, 1j, 3c, 3d, 4d (45%), C–E: Ann.
<i>Erythrotrichia carnea</i> (Dillwyn) J. Agardh	III, IV, VI, 1, 4, 5, 8, 9, 16, 1j (20%), C–E: Ann.
<i>Euthora cristata</i> (L.) J. Agardh	I, III, IV, VI, VII, 1, 4, 5 (16%), C–E: Per.
<i>Fimbrifolium dichotomum</i> (Lepeschkin) G. I. Hansen	IV, VII (4%), C: Per.
<i>Gloiosiphonia capillaris</i> (Hudson) Berkeley	I (2%), C: Ann.
<i>Gymnogongrus crenulatus</i> (Turner) J. Agardh	I, IV (4%), C: Per.
<i>Harveyella mirabilis</i> (Reinsch) F. Schmitz <i>et</i> Reinke	I (2%), C: Per.
<i>Hildenbrandia rubra</i> (Sommerfelt) Meneghini	II, IV, VI, VII, 1, 3, 4, 6–9, 13, 14, 16, 17, 1g, 1i, 1j, 3c, 3d, 4a (41%), C–E: Per.
<i>Lithothamnion glaciale</i> Kjellman	I, III, IV, VII (8%), C: Per.
<i>Lomentaria orcadensis</i> (Harvey) Collins <i>ex</i> W. R. Taylor	I (2%), C: Per.
<i>Mastocarpus stellatus</i> (Stackhouse <i>in</i> Withering) Guiry	I–V, VII, 3, 4, 1g, 1j, 4b (20%), C–E: Per.
<i>Membranoptera alata</i> (Hudson) Stackhouse	I, IV, VI, VII (8%), C: Per.
<i>Palmaria palmata</i> (L.) Kuntze	I, II, IV, VII (8%), C: Per.
“ <i>Petrocelis cruenta</i> J. Agardh”	I, IV, V (6%), C: Per.
<i>Peyssonnelia rosenvingii</i> F. Schmitz <i>in</i> Rosenvinge	II, IV, VI, VII, 6, 16, 1i, 1j (16%), C–E: Per.
<i>Phycodrys rubens</i> (L.) Batters	I–IV, VI, VII, 4, 5 (16%), C–E: Per.
<i>Phyllophora pseudoceranoides</i> (S. G. Gmelin) Newroth <i>et</i> A. R. A. Taylor	I, III–VII, 1, 3, 4 (18%), C–E: Per.
<i>Phymatolithon laevigatum</i> (Foslie) Foslie	I, IV, V (6%), C: Per.
<i>Phymatolithon lamii</i> (Me. Lemoine) Y. M. Chamberlain	IV (2%), C: Per.
<i>Phymatolithon lenormandii</i> (Areschoug <i>in</i> J. Agardh) W. H. Adey	II, IV, V, 1i, 1j, 4b (12%), C–E: Per.

Table 1. Continued.

	Collection Sites, % Occurrence, and Longevity
<i>Plumaria plumosa</i> (Hudson) Kuntze	I (2%), C: Per.
<i>Pneophyllum fragile</i> Kützing	IV (2%), C: Per.
<i>Polyides rotundus</i> (Hudson) Greville	I, IV, VII (6%), C: Per.
<i>Polysiphonia flexicaulis</i> (Harvey) Collins	I, IV, VII, 5 (8%), C–E: Per.
<i>Polysiphonia fucoides</i> (Hudson) Greville	I, II, IV, 2, 4, 8, 9, 1j (16%), C–E: Per.
<i>Polysiphonia harveyi</i> Bailey	I–VII, 1, 3–5, 7–9, 16, 17, 1j (33%), C–E: Ann.
<i>Polysiphonia lanosa</i> (L.) Tandy	I–VII, 4, 16 (18%), C–E: Per.
<i>Polysiphonia nigra</i> (Hudson) Batters	4 (2%), E: Per. (?)
<i>Polysiphonia stricta</i> (Dillwyn) Greville	I, IV, V (6%), C: per.
<i>Porphyra amplissima</i> (Kjellman) Setchell et Hus in Hus	IV (2%), C: Ann.
<i>Porphyra leucosticta</i> Thuret in Le Jolis	I, IV, VII, 4, 1j (10%), C–E: Ann.
<i>Porphyra linearis</i> Greville	I, IV–VII, 1, 5 (14%), C–E: Ann.
<i>Porphyra miniata</i> (C. Agardh) C. Agardh	I, IV (4%), C: Ann.
<i>Porphyra purpurea</i> (Roth) C. Agardh	4a (2%), E: Ann.
<i>Porphyra umbilicalis</i> (L.) Kützing	I, IV, V, VII, 1 (10%), C–E: Ann.
<i>Porphyropsis coccinea</i> (J. Agardh ex Areschoug) Rosenvinge	IV (2%), C: Ann.
<i>Ptilota serrata</i> Kützing	I, III, IV, VI, VII, 1, 4, 5 (16%), C–E: Per.
<i>Rhodomela confervoides</i> (Hudson) P. C. Silva	I, IV, V (6%), C: Per.
<i>Scagelia pylaisaei</i> (Montagne) M. J. Wynne	I, IV (4%), C: AAnn.
<i>Titanoderma corallinae</i> (Crouan frat.) Woelkerling, Y. M. Chamberlain et P. C. Silva	V (2%), C: Per.
<i>Titanoderma pustulatum</i> (J. V. Lamouroux) Woelkerling	I, IV, V, VII (8%), C: Per.
“ <i>Trailliella intricata</i> Batters”	I, IV, 4 (6%), C–E: Per.
TOTAL RED ALGAL TAXA = 61	
TOTAL SEAWEED TAXA = 148	

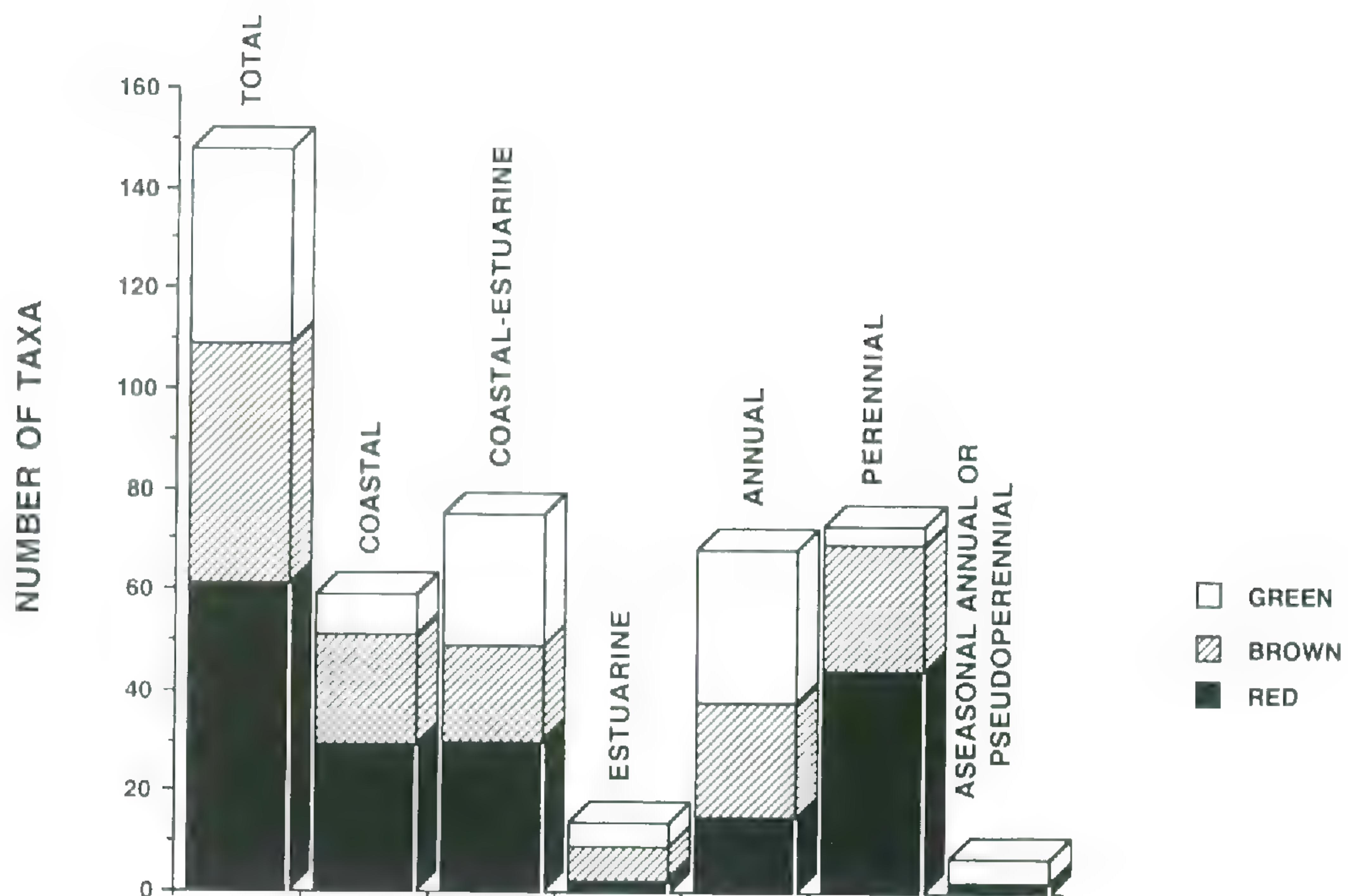


Figure 7. Patterns of species richness, local distribution, and longevity of seaweed taxa from six coastal and estuarine habitats within southern Maine.

(2.0% occurrence); 23 (7 green, 9 brown, and 7 red algae) occurred at two locations (3.9% occurrence); and 23 (8 green, 7 brown, and 8 red algae) were found at three sites (5.9% occurrence). The most ubiquitous taxa are outlined in Figure 9.

Floristic comparisons. Figure 10 illustrates patterns of species richness and floristic similarities between nearby coastal habitats, the main channel and the four tributaries of BBH (cf. Appendix). The highest total (Figure 10A) and mean number of taxa (Figure 10B) occurred on the open coast (134 taxa; 91%). The main channel had 83 taxa (56%), while the tributaries had the following number and % of total taxa: #1: 42 taxa, 28%; #4: 26 taxa, 18%; #3: 24 taxa, 16%; #2: 6 taxa, 4%. The mean number of total and shared taxa/habitat (Figure 10C) have similar patterns. The highest and most variable numbers occur on the open coast ($\bar{x} = 59.5 \pm 35.7$ and 47.3 ± 47.97 for total and shared taxa, respectively), and the lowest for tributary #2 ($\bar{x} = 3.0 \pm 0$ and 4.7 ± 1.21 , for total and shared taxa, respectively). Patterns for mean percentage of shared taxa (Figure 10D) contrast with the above. The open coast and tributary #2 have the lowest percentages ($\bar{x} = 43.6 \pm 33.8\%$ and $33.4 \pm 35.4\%$, respectively),

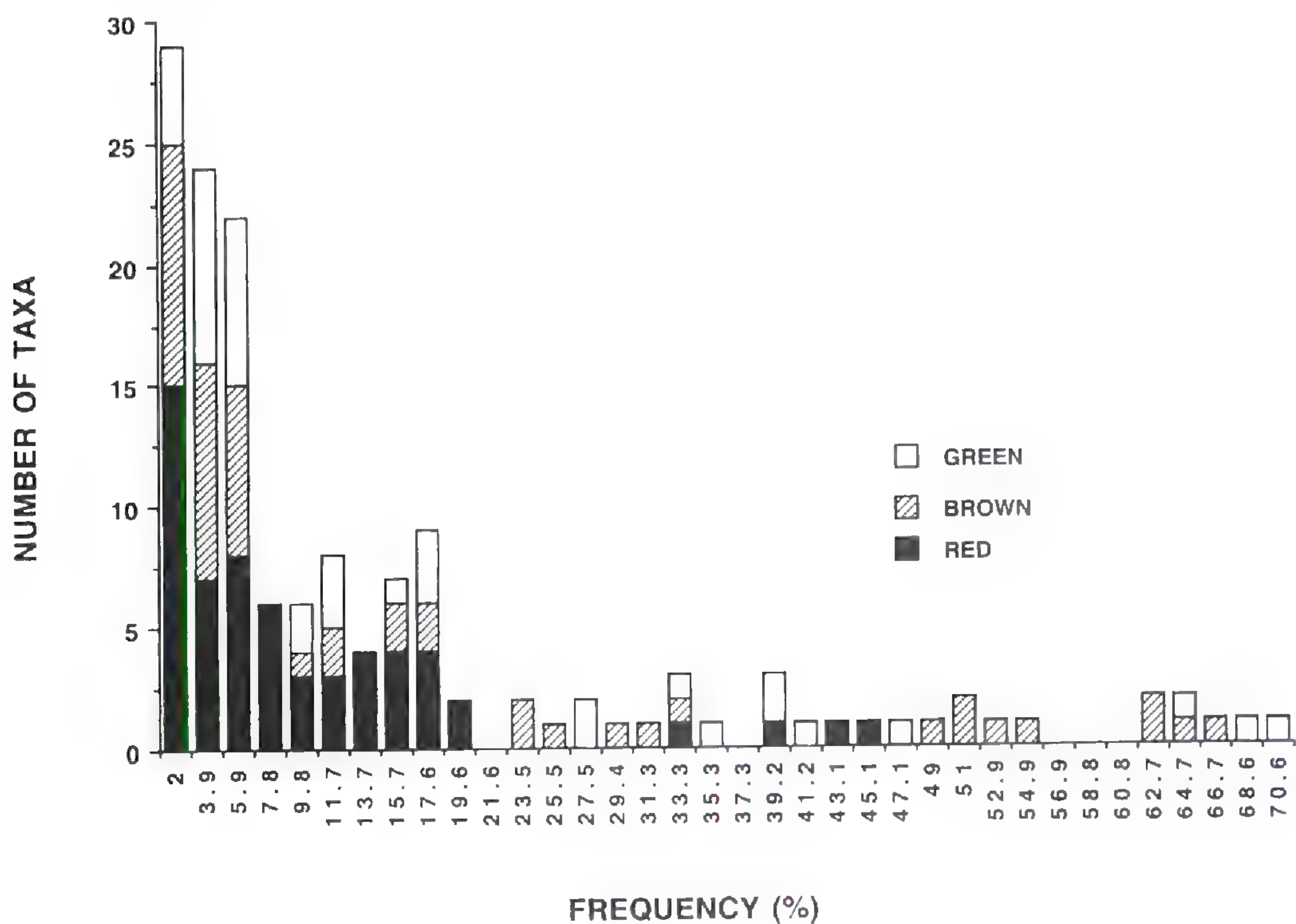


Figure 8. Frequency distribution patterns of 148 seaweed taxa recorded from fifty-one open coastal and estuarine sites in southern Maine. Taxa found at only one site (2% occurrence) are represented by the extreme left bar of the graph; those found at only two (3.9%) are represented by the next bar, etc.

while tributaries #1, #3, and #4 have the highest percentages ($\bar{x} = 55.6 \pm 27.9\%$ to $59.0 \pm 28.7\%$).

Intra-habitat patterns of species richness were highly variable (Figures 11–13). Exposed open coastal areas of Nubble Light and Seapoint exhibit peak values of 102 and 117 taxa, respectively, while Sister's Point and Swards Cove are the most depauperate with 36 taxa each (Figure 11). In the main channel of BBH (Figure 12) the highest numbers of seaweeds/site occurred just inside the mouth (sites #4 and #5), while the lowest occurred near tidal limits (site #21). Green and brown algae (particularly furoid taxa) were widely distributed, while the reds were more circumscribed. Greens dominated inner habitats (sites #18 to #21).

Figure 13 depicts species richness in BBH's four tidal tributaries. Tributary #1 showed an enhancement of species numbers and red algae inland from the Harbor mouth. This contrasts with the pattern observed in the main channel. Site #1j is an estuarine tidal rapid with 35 taxa; it is located about 2.0 km inland from

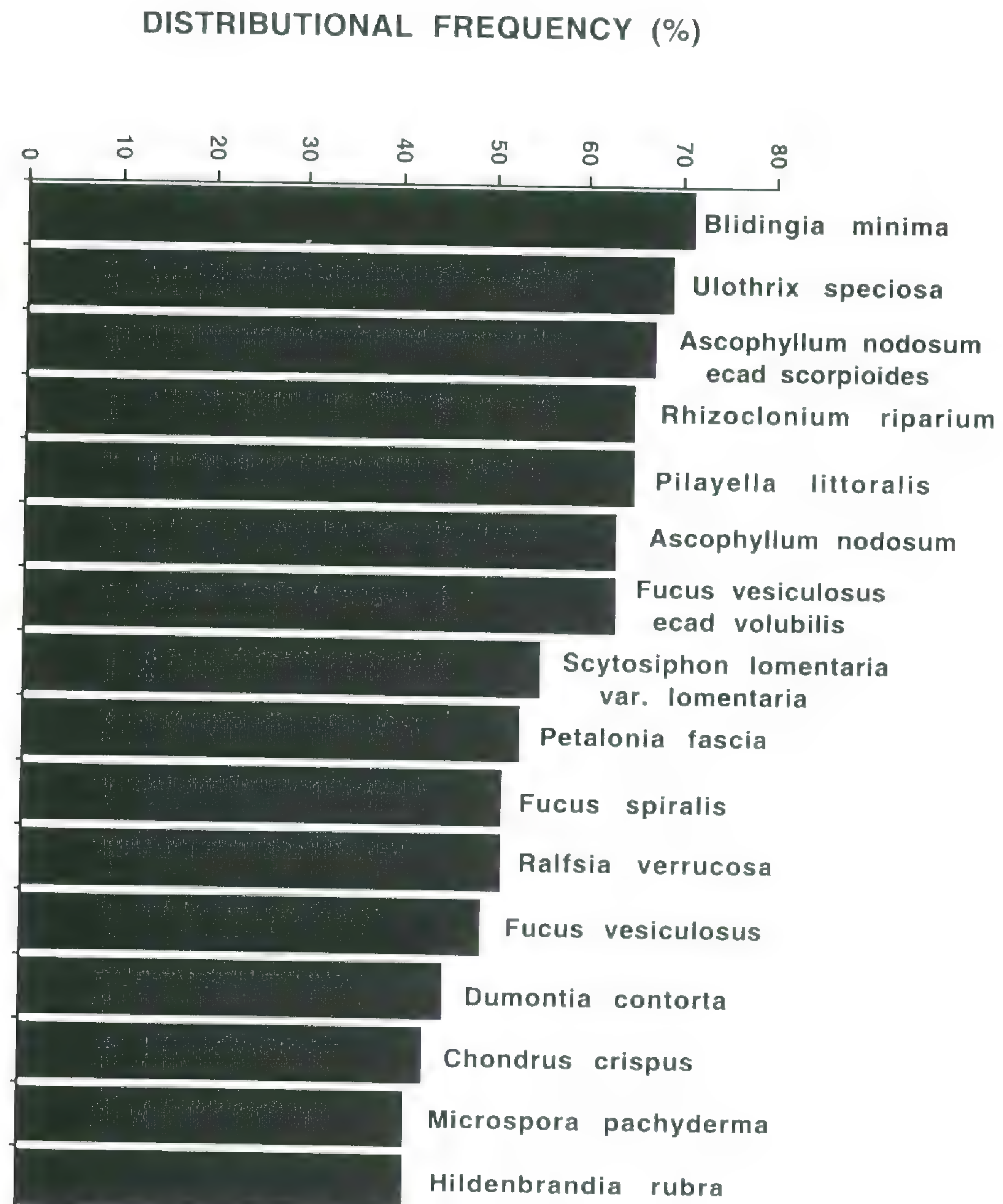


Figure 9. Distributional frequency (%) of the sixteen most common seaweed taxa at the fifty-one study sites.

the open coast via the Harbor mouth and 2.7 km inland from Swards Cove on Gerrish Island (cf. Appendix). Species richness and composition in #3 was lower but analogous to #1. Tributary #2 had the lowest diversity, while #4 had a similar (but reduced) pattern to that of the main channel.

Figure 14 compares the mean number ($\pm$ SD) of taxa/site in BBH's main channel and four tributaries, plus 17 other estuaries. The mean number of taxa in BBH's main channel ($\bar{x}$ = 20.7 $\pm$

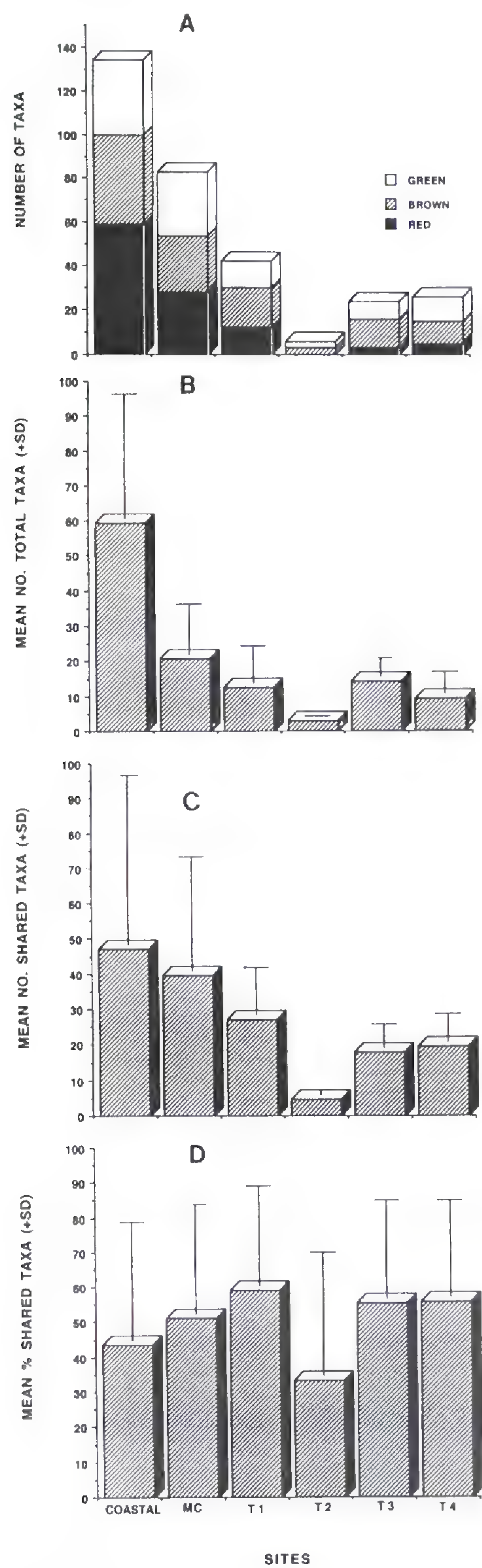


Figure 10. A comparison of the seaweed florae from six coastal sites (COASTAL), the main channel (MC), and four tributaries (#1–4) of Brave Boat Harbor. Four patterns are shown: (A) number of total red, brown, and green seaweeds; (B) mean number of total taxa; (C) mean number of shared taxa; (D) mean percentage of shared taxa. All bars are ± 1 SD. See Appendix for habitat descriptions and abbreviations.

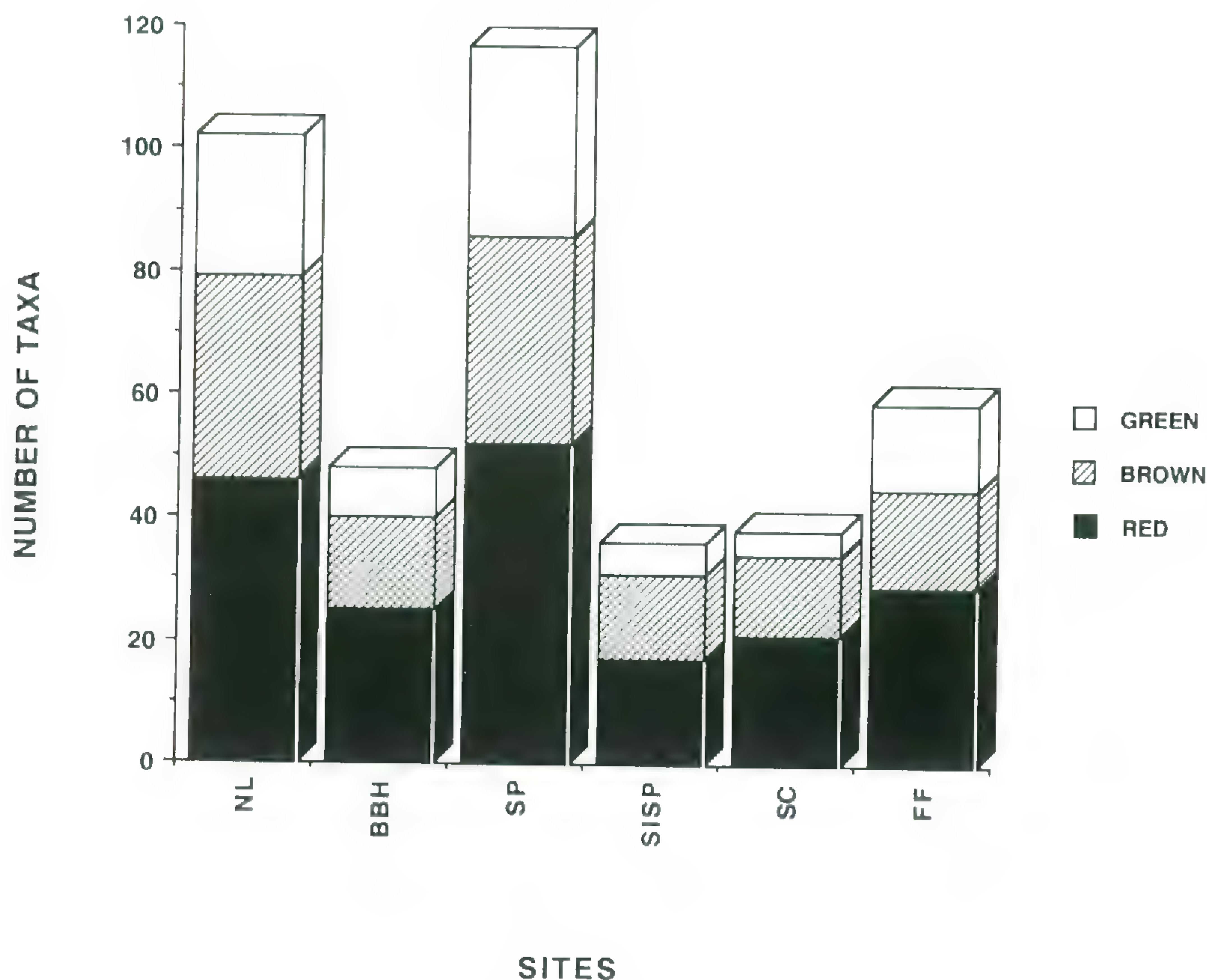


Figure 11. The number of total seaweed taxa at six nearshore open coastal sites from Cape Neddick to Fort Foster. See Appendix for habitat descriptions and abbreviations.

14.4) is less than in the Piscataqua River and Little Bay, while it is approximately the same as in the York River ($\bar{x} = 21.4 \pm 3.2$) and Great Bay proper ($\bar{x} = 25.3 \pm 24.9$). The main channel of BBH has a higher mean number of taxa than the following sites: (1) the four contiguous tributaries near BBH that vary from $\bar{x} = 3.0 \pm 0$ to 14.3 ± 5.1 ; (2) several mid- and inner-estuarine sites such as the Oyster River ($\bar{x} = 12.6 \pm 7.9$) and Winnicut River ($\bar{x} = 1.3 \pm 1.6$) of the Great Bay Estuary System; (3) the Hampton-Seabrook Estuary ($\bar{x} = 10.5 \pm 5.5$); (4) the Merrimack River Estuary ($\bar{x} = 3.5 \pm 5.2$). The large standard deviations recorded for the main channel of BBH, the Piscataqua River, Little Bay, and Great Bay indicate that these areas are more spatially variable than the York River and other inner estuarine habitats described above.

Longevity patterns. Sixty-eight of the 148 taxa recorded (46%) are annuals, 73 (49%) perennials, and 7 (5%) either asea-

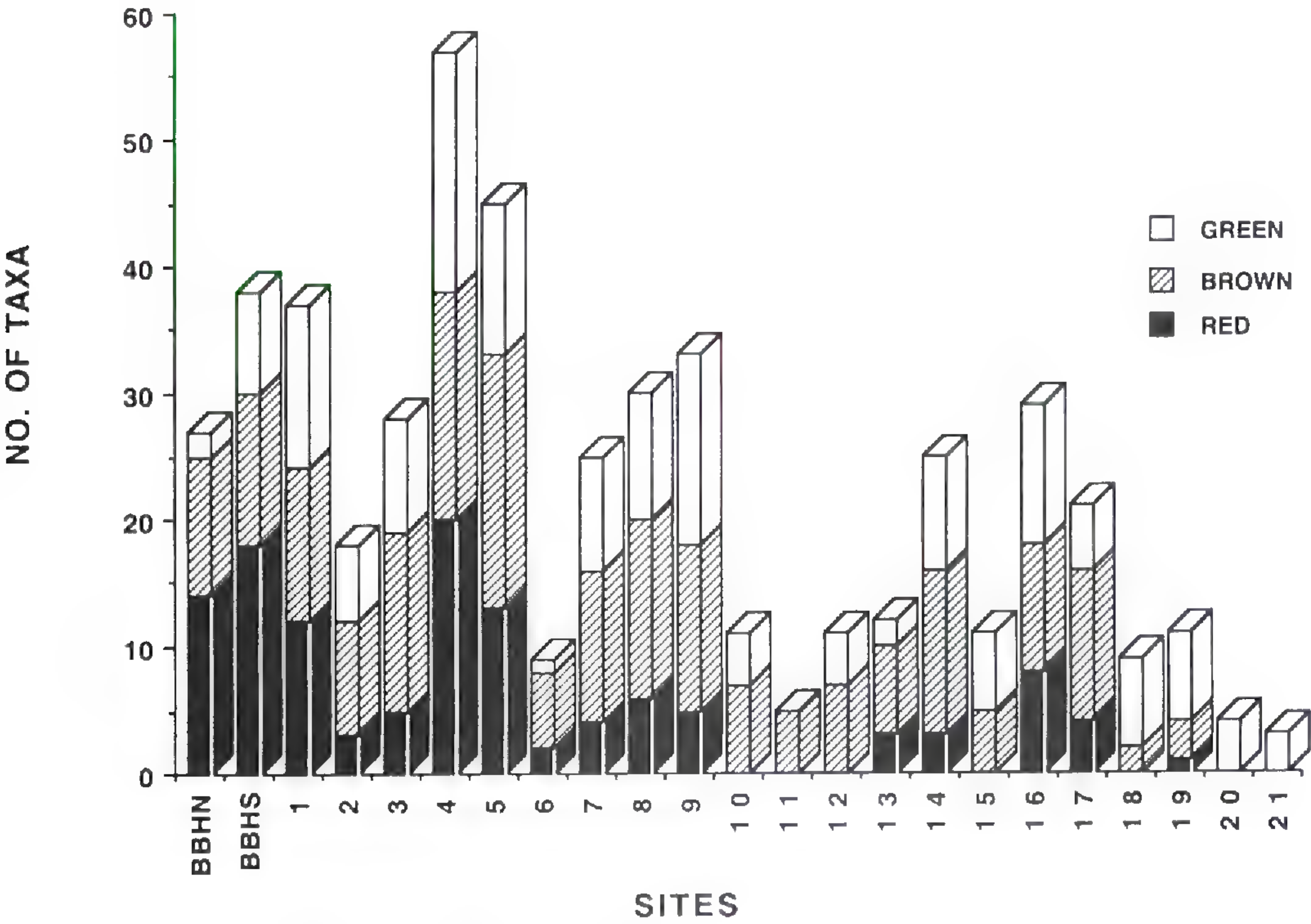


Figure 12. The number of seaweed taxa at twenty-one sites within the main tidal channel of Brave Boat Harbor and the harbor entrance (BBHN and BBHS). See Appendix for habitat descriptions.

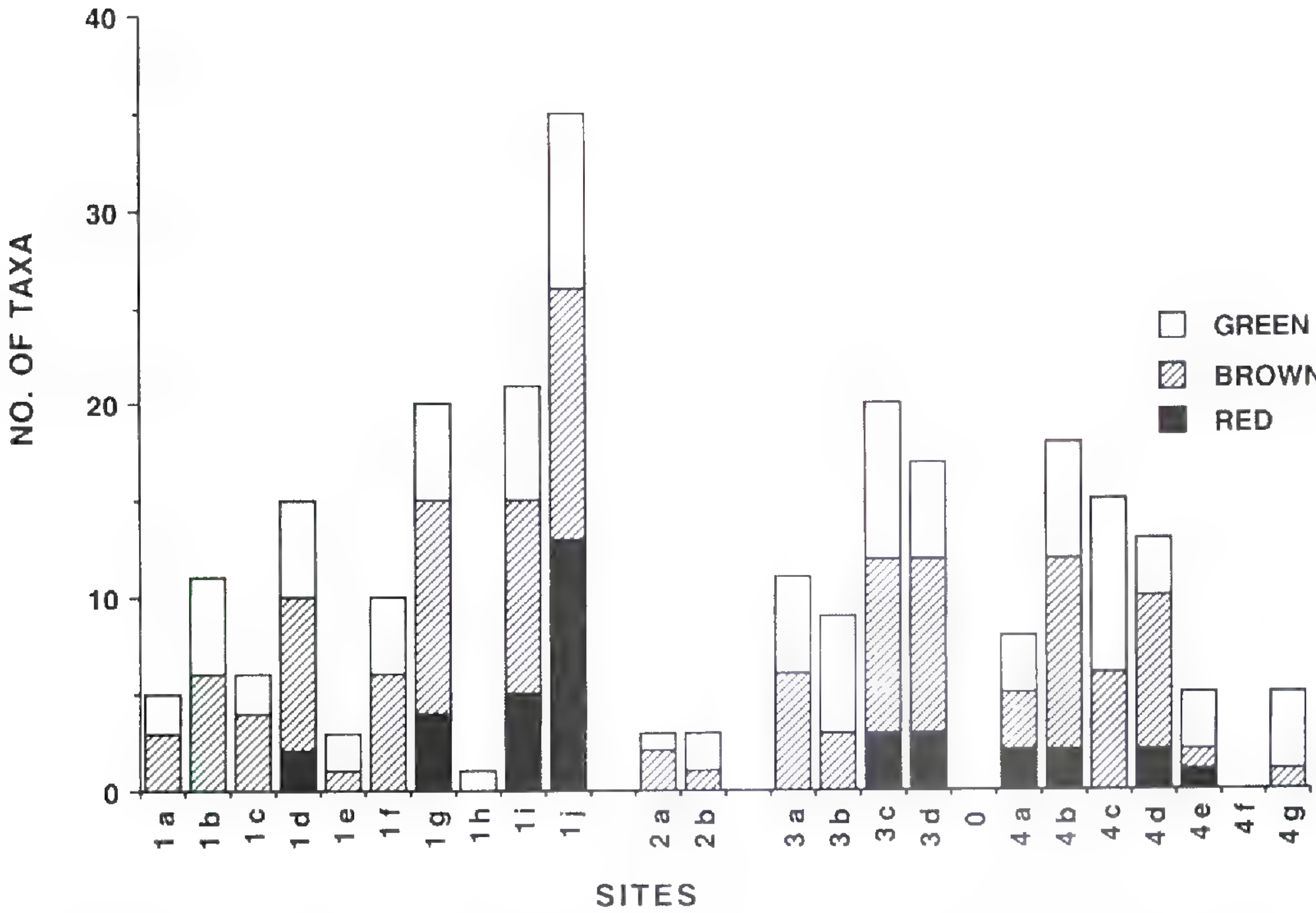


Figure 13. The number of seaweed taxa at multiple sites within four contiguous tidal tributaries (#1–4) in Brave Boat Harbor. See Appendix for habitat descriptions.

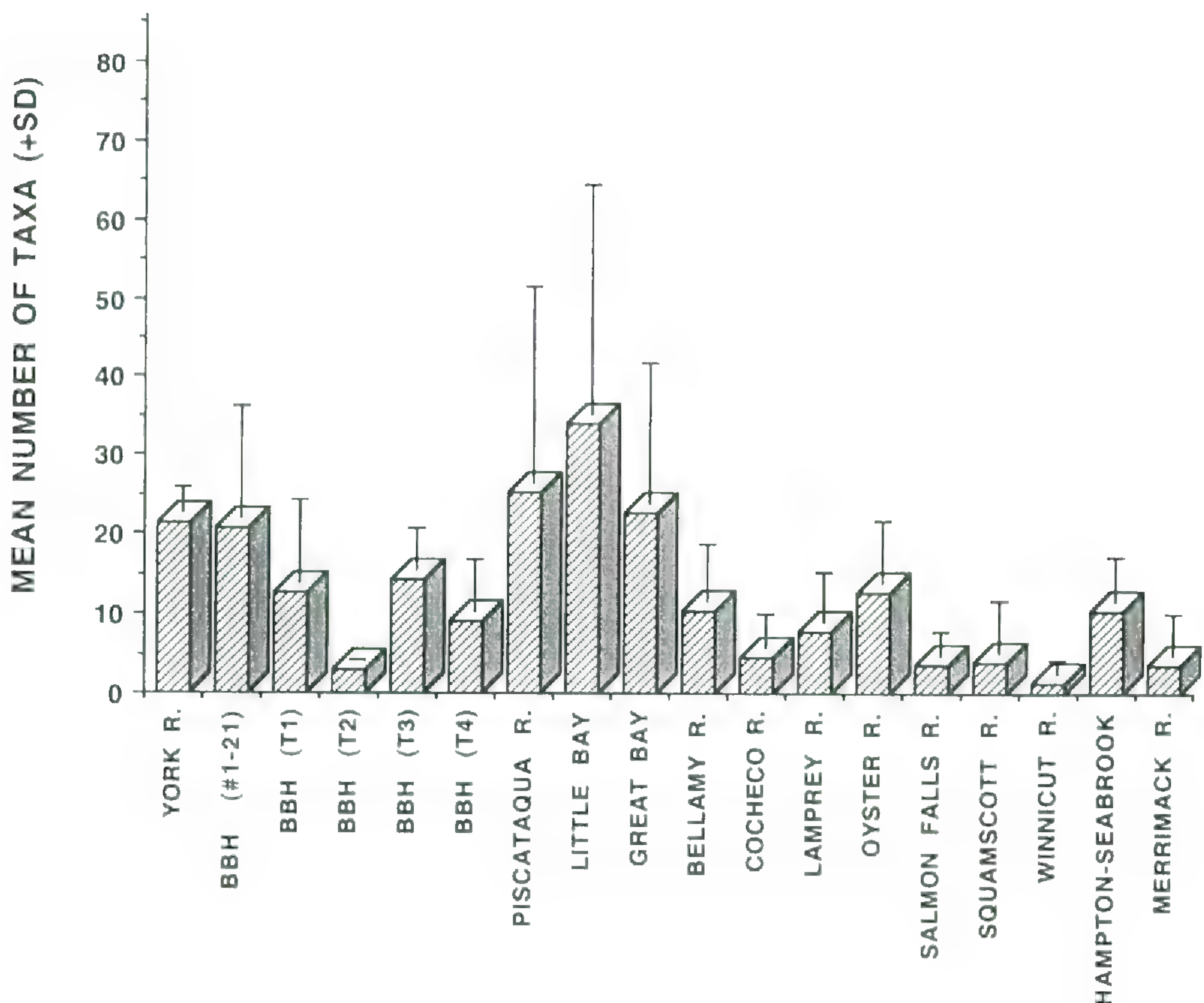


Figure 14. Mean ($\pm$ SD) number of seaweed taxa/site within Brave Boat Harbor and fourteen other estuaries from southern Maine (York River) to Massachusetts (Merrimack River). See the text for a synopsis of number of collection sites/area.

sonal annuals or pseudoperennials (Table 1; Figure 7). Approximately three-quarters of the green algae (30 taxa, 77%), one-half of the browns (23 taxa, 48%), and one-quarter of the reds (15 taxa, 25%) are annuals. The ratios of annuals to perennials (Figure 15A, B) are analogous to those previously described, showing only modest differences: (1) open coast, 63/134, 47%; (2) BBH main channel, 43/83, 51.8%; (3) tributary #1, 18/42, 42.8%; (4) tributary #2, 3/6, 50%; (5) tributary #3, 14/24, 58.3%; (6) tributary #4, 13/26, 50%.

DISCUSSION

Species richness within the 51 southern Maine sites is relatively high (148 taxa) compared with other Northwest Atlantic sites. For example, 216 taxa are recorded from over 200 coastal and estuarine sites in New Hampshire and southern Maine

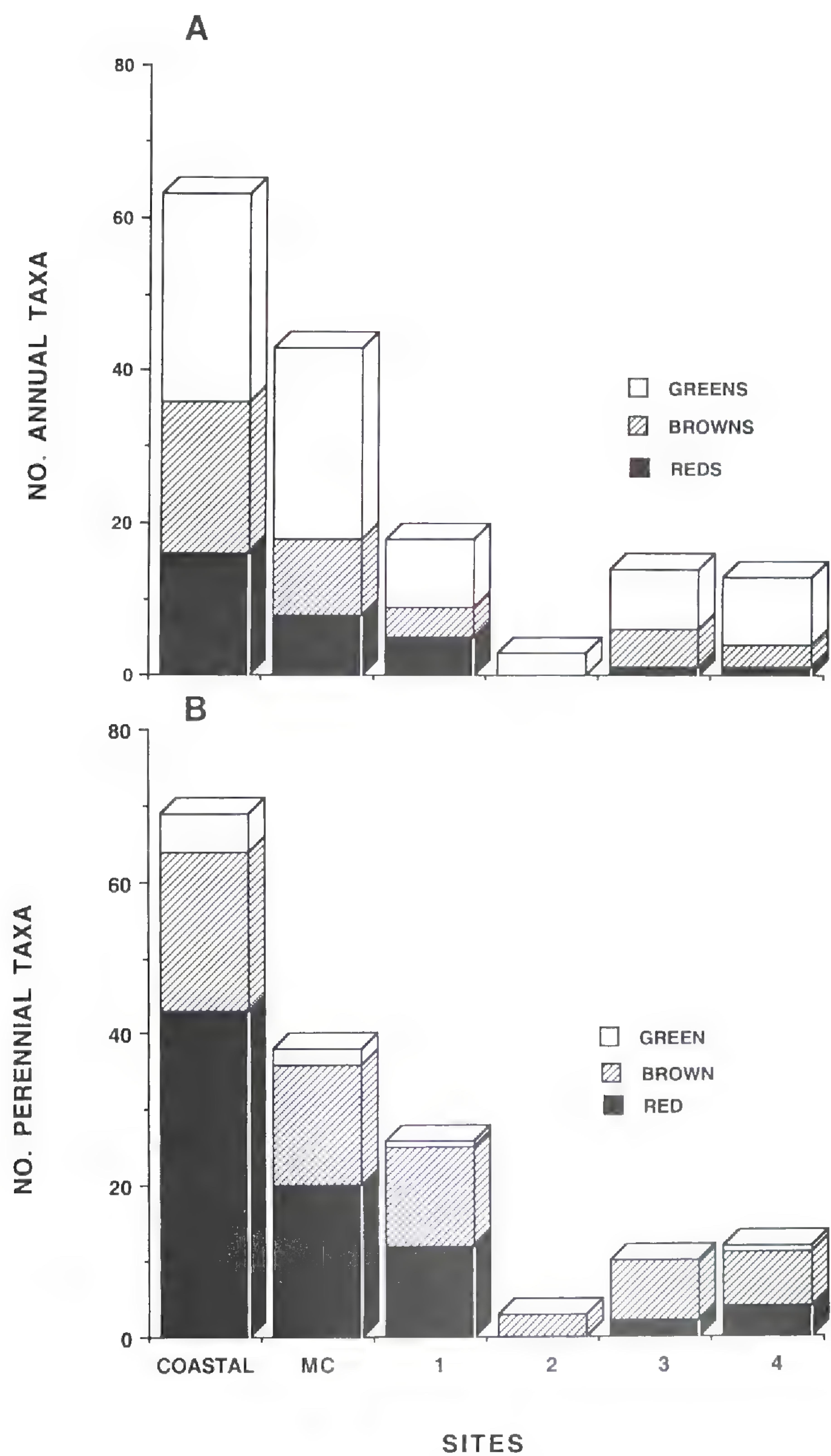


Figure 15. A comparison of the number of annual (A) and perennial (B) red, brown, and green seaweeds from six coastal sites (COASTAL), the main tidal channel (MC), and four tributaries (#1–4) of Brave Boat Harbor. See Appendix for habitat descriptions and abbreviations.

(Mathieson and Hehre 1986), which include 179 taxa from the nearshore open coast between Portsmouth and Seabrook (NH), 164 from the Isles of Shoals (ME and NH), 161 from the Great Bay Estuary System (NH and ME), and 63 from the Hampton-Seabrook Estuary System (NH). Although the numbers recorded for the Shoals and Great Bay Estuary System are similar, their species composition is quite different, presumably because of pronounced habitat variations (Mathieson and Penniman 1986b). Maine's two largest embayments (Penobscot and Casco Bays) have 139 and 194 taxa, respectively (Collins 1911; Farlow 1881; Mathieson et al. 1996). The numbers of taxa from insular habitats throughout the Gulf of Maine range from 145 on Mount Desert, the largest coastal island (Collins 1894; Mathieson et al. 1998), to 136 on Smuttynose Island, Maine, and 4–65 taxa/island in Penobscot Bay (Mathieson et al. 1996, 1998). Penikese Island, just south of Cape Cod, Massachusetts, has 131 taxa (Doty 1948; Jordan 1874; Lewis 1924). Newfoundland, the largest and most extensively studied northeastern Canadian island, has about 254 taxa (South 1983; South and Hooper 1980), while Tittley and colleagues (1987) have recorded 159 taxa from Passamaquoddy Bay, New Brunswick, Canada.

There is a conspicuous reduction in species richness within the six southern Maine habitats (Figure 10); the highest numbers of taxa and perennial seaweeds occur on the open coast. A combination of physical factors is probably responsible, including enhanced water motion, greater availability of rocky substrata, and more stable hydrographic conditions (Coutinho and Seeliger 1984; Doty and Newhouse 1954; Hartog 1971; Josselyn and West 1985; Ketchum 1983; Mathieson and Penniman 1986a, 1991; Wilkinson 1980). Brave Boat Harbor is more turbid and sedimented and has greater hydrographic variability than the nearby open coast (Figures 5 and 6). Inner estuarine areas of BBH have steep tidal channels and dissected salt marshes, which are dominated by reduced floras of ephemeral (opportunistic) green algae (Table 1). Physical extremes probably determine the distributional limits and potential for perennial longevity where physiological tolerances are approached (cf. Fraclik and Mathieson 1975; Guo and Mathieson 1992; Kinne 1970, 1971; Penniman and Mathieson 1985). For example, within the inner reaches of the Great Bay Estuary (i.e., Great Bay proper) hydrographic variability is approximately two (temperature) to five times (salinity) greater

than on the adjacent open coast near Portsmouth (Loder et al. 1979, 1983a, 1983b; Norall et al. 1982). Similar, but more circumscribed patterns are present in the BBH area (cf. Figures 5 and 6), and seasonal extremes in temperature and salinity are evident in the Harbor's interior. Unlike the land-locked and muddy inner parts of the Great Bay Estuary, the outer third of BBH is directly connected to the open ocean and has a sandy substratum. Thus, BBH's flora consists of many oceanic species at its mouth and a few estuarine ones at its tidal limits.

A comparison of the mean number of taxa/site in BBH and the York, Piscataqua, and Merrimack Rivers, is instructive as all four estuaries are contiguous with the open coast and in close proximity (Figures 1 and 14). The York River and BBH exhibit similar patterns, the Piscataqua River is more diverse, and the Merrimack River is very depauperate. There are varying levels of eutrophication and development in the four estuaries: BBH has circumscribed fecal coliform contamination (see above); the York River has limited housing development and eutrophication; and the Piscataqua and Merrimack Rivers have intermediate to high levels of industrial development and eutrophication, respectively (cf. Mathieson and Fralick 1973; Mathieson and Penniman 1986a; Mathieson, Reynolds, and Hehre 1981; Mathieson et al. 1993). The Merrimack River is one of the most polluted in New England and is also one of the major sources of fresh water discharge into the Gulf of Maine (Anonymous 1984, 1987; Appolonio 1979; Jerome et al. 1965; Miller et al. 1971). Within the same four estuaries, the Piscataqua River has the greatest diversity of habitats, with tidal rapids, salt marshes, and stable substrata, all of which combine to support a diverse seaweed flora. In summary, the mean number of taxa/site in BBH exceeds the values for the Merrimack River, the contiguous BBH tributaries, and several mid- and inner-estuarine sites. Low species diversity is a typical response to stresses such as pollution, development, and extreme hydrographic variability where only a few tolerant ulotrichalean green algae such as *Enteromorpha*, *Monostroma*, *Ulva*, and *Ulvaria* dominate (Cotton 1910; Fritsch 1935; Sawyer 1965; Wilkinson 1980).

Intra-habitat diversity patterns are determined by the same suite of physical factors. Differential wave action, stability of substrata, and habitat variability are key factors determining spatial differences of coastal communities (Mathieson et al. 1991). The ex-

treme variability of floras at Seapoint and the mouth of Brave Boat Harbor (BBHN and BBHS) is a case in point (Figure 11), with both sites exposed to strong wave action. Seapoint has a greater diversity of habitats and rocky outcrops and the mouth of BBH is dominated by cobbles and boulders that move in storms (cf. Appendix). The higher diversity of seaweeds in BBH's main channel compared with its tributaries may also be explained by differential availability of solid substrata and varying hydrographic conditions. The main channel has scattered boulders, rocks, and pebbles, plus the remains of an old wooden railroad trestle; the tributaries have more limited and scattered solid substrata (particularly #2). Sporadic peaks of species diversity are probably associated with enhanced substrata and water motion. For example, the highest number of species in tributary #1 occurs at the bridge culvert on Seapoint Road (#1j), where strong currents, abundant rocks, and a fringing marsh are present. By contrast, sites #1h and #1i are impounded and do not totally drain at low tide, reducing the numbers of taxa. Sporadic patterns are evident in the third and fourth tributaries, where localized populations of *Chondrus crispus*, *Dumontia contorta*, and *Hildenbrandia rubra* grow in narrow tidal channels with strong currents and rocky substrata (cf. Table 1; Figure 13). As noted by Lewis (1964, 1968) tidal rapids have high concentrations of dissolved gases (oxygen and carbon dioxide) and reduced sediments, which allow enhanced colonization by open coastal and perennial seaweeds (Mathieson et al. 1977, 1983; Reynolds and Mathieson 1975).

Seaweed longevity patterns in BBH reflect the above-described physical factors. Outer floras are dominated by perennial taxa, while annuals exhibit broader distributions, often dominating inner estuarine habitats. *Blidingia minima*, *Enteromorpha* spp., *Microspora pachyderma*, and *Rhizoclonium riparium* are conspicuous annual green algae that form extensive mats amongst marsh grasses. Perennial greens are few in number and primarily occur in the main channel or in deep outer pools (*Codium*). Perennial brown and red algae (e.g., *Ascophyllum nodosum*, *Laminaria saccharina*, *Chondrus crispus*, *Hildenbrandia rubra*, *Phymatolithon lenormandii*, and *Polysiphonia fucoides*) exhibit either analogous coastal patterns or are found in localized areas of strong tidal currents. Conspicuous annuals include *Dumontia contorta*, *Melanosiphon intestinalis*, *Petalonia fascia*, and *Scytosiphon lomentaria* var. *lomentaria*.

The fucoid algae found in BBH are of special interest because of their diversity, habitat preferences, and abundance. Prior to the discovery of the “muscoïdes-like” *Fucus* from sandy outer habitats in BBH, it was unknown from the Northwest Atlantic (cf. Sears 1998; South and Tittley 1986; Wynne and Magne 1991). The plant is a miniature alga that lacks a holdfast and forms an embedded turf or “moss-like carpets” (Norton and Mathieson 1983) in sandy sediments associated with *Spartina patens*. The ecology of *F. spiralis* in BBH is unique as it grows abundantly on outer sandy bluffs (i.e., psammophytically). By contrast, in nearby muddy estuaries (e.g., the Great Bay Estuary System), it only grows attached to scattered metamorphic and volcanic rock outcrops (Niemeck and Mathieson 1976). Attached populations of *F. vesiculosus* are restricted to scattered boulders and pilings (Table 1).

As noted above, three detached fucoid ecads are common in BBH, *Ascophyllum nodosum* ecad *scorpioides*, *Fucus vesiculosus* ecad *volubilis*, and *F. spiralis* ecad *lutarius*. The first two are the most abundant and widely distributed (Table 1), growing as entangled and/or embedded populations amongst culms of *Spartina alterniflora*. *Fucus spiralis* ecad *lutarius* occupies a similar habitat, but it is scattered and less abundant. Detached plants of *Fucus*, variously described taxonomically, have been reported since the 1880s from Long Island, New York, to Massachusetts (Taylor 1957). After comparing European materials, Chapman (1939) confirmed the presence of *F. spiralis* ecad *lutarius* from Scituate, Massachusetts, and *F. vesiculosus* ecad *volubilis* from Cold Spring Harbor, Long Island, New York, with the latter being based upon collections of Baker and Blandford in 1912. Chapman (1939) notes that few investigators record both detached *Fucus* ecads in New England salt marshes (cf. Webber and Wilce 1971). This generalization is particularly true for marshes north of Massachusetts; our investigations throughout Maine (Mathieson, Dawes, and Hehre, unpubl. data) indicate that both ecads are widely distributed within the state’s salt marshes.

The introduced green alga *Codium fragile* subsp. *tomentosoides* is rare at nearshore coastal sites in New Hampshire and Maine (cf. Mathieson and Hehre 1986; Mathieson et al. 1993). However, it grows abundantly at several insular sites in the Gulf of Maine (e.g., the Isles of Shoals) but is previously unknown from estuarine habitats (Harris and Mathieson, in press). The occurrence of *Codium*

in BBH ponds represents the first record of its abundant growth in a Maine salt marsh. The microscopic green alga *Urospora curvata* is newly recorded from nearshore coastal areas in Maine, being previously known from deep water habitats within the Gulf of Maine and southern Massachusetts (Grocki 1984; Sears and Cooper 1978). We found it growing epiphytically on *Ascophyllum nodosum* and *Fucus vesiculosus* at both Seapoint and BBH. The opportunistic brown alga *Melanosiphon intestinalis* is very prolific within BBH, particularly on slumping channel embankments. It is a seasonal annual that is most conspicuous during spring and early summer, being reduced in size and confined to small residual patches by mid-July. The plant also grows abundantly in many other Maine and New Hampshire tidal marshes (Mathieson, Dawes, and Hehre, unpubl. data), while it is uncommon at contiguous open coastal sites within the same two states. By contrast, *Melanosiphon* exhibits a broader coastal distribution in Massachusetts and southern New England (C. Schneider, pers. comm.).

In summary, the coastal and estuarine seaweed flora of southern Maine is highly diverse and exceeds or equals that of other northern New England regions, such as Penobscot Bay (Mathieson et al. 1996) and Mount Desert Island (Mathieson et al. 1998). Detached fucoid ecads and psammophytic populations of *Fucus spiralis* are common in BBH. New records for the “muscoide-like” *Fucus* and for *Urospora curvata* and *Codium fragile* subsp. *tomentosoides* are given.

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APPENDIX

A SYNOPSIS OF STUDY SITES WITHIN SOUTHERN MAINE

OPEN COASTAL SITES (York and Kittery; Figure 2)

- I. Cape Neddick (CN), Nubble Light. An exposed site with substrata consisting of massive outcrops and boulders grading into sand.
- II. North bank of Brave Boat Harbor mouth (BBHN), York. An exposed open site with extensive boulders and relatively few rock outcrops and tide pools.
- III. South bank of Brave Boat Harbor mouth (BBHS), Kittery. An exposed open site composed of coarse gravel and cobbles with few rock outcrops and tide pools. A highly dissected fringing marsh is also present.
- IV. Seapoint (SP), Kittery. A semi-exposed spit of land on the seaward side of Cutts Island that experiences anthropogenic trampling year-round. The substrata are composed of rock outcrops, scattered boulder fields, sand, and cobbles; many tide pools are present at different elevations. The upper littoral zone slope changes with extensive seasonal sand deposition and erosion.
- V. Sisters Point (SISP), Gerrish Island, Kittery. A semi-exposed site; substrata of boulders, cobbles, and scattered rock outcrops.
- VI. Swards Cove (SC), Gerrish Island, Kittery. A semi-exposed site; substrata the same as Sister's Point.
- VII. Fort Foster (FF), Gerrish Island, Kittery. An outermost estuarine site (ca. 0.1 km inland) on the Piscataqua River, northeast of Wood Island. The substrata consist of scattered rock outcrops, boulders, cobbles, fragmented shale, and scattered fringing marshes.

BRAVE BOAT HARBOR (Figure 3)

Main Tidal Channel (i.e., between BBHN and BBHS). The northern side of the main channel is in York, while the southern side is in Kittery (km = distance inland from mouth).

1. York side of outer harbor (0.1 km). Cobbles and pebbles are present, plus a small, highly dissected fringing marsh.
2. York side of outer harbor (0.3 km). Situated near a sandy embayment (a flood tidal delta), downstream from old bridge pilings. Beds of blue mussels (*Mytilus edulis*) are present, as well as scattered small rocks and an expansive high salt marsh habitat. The latter shows extensive slumping.
3. Kittery side of outer harbor on Cutts Island (0.37 km) behind a coastal berm that forms a sandy embayment (a flood tidal delta). There are high and fringing marshes, scattered bedrock, and an extensive boulder field with a sharp slope (ca. 70°). At low tide, fresh water runoff from the high marsh flows into the central channel and out to the sandy embayment.
4. Kittery side of outer harbor (0.38 km). Upstream from a set of old

bridge pilings and near the mouth (W side) of tributary #1, which delineates Cutts Island.

5. Kittery side of outer harbor on Cutts Island (0.39 km). Next to a set of old bridge pilings and near the mouth of tributary #1. The pilings provide an excellent substratum for seaweeds and are located in an area of tidal currents. Deep pools support a variety of seaweed taxa. Extensive slumping and erosion of the marsh is evident.
6. York side of outer harbor (0.40 km). There is a fringing marsh, located within a sandy embayment (a flood tidal delta) on the backside of a coastal berm.
7. York side of outer harbor near old bridge pilings (0.42 km).
8. Kittery side of outer harbor (0.48 km). The site is located on Cutts Island behind a coastal berm within a sandy embayment (a flood tidal delta).
9. Kittery side of harbor (0.65 km). The high marsh has slumped and exposed the remains of old wooden pilings and tree stumps, providing habitats for various seaweeds. The tidal slopes and channels are muddy with a little sand.
10. York side of harbor near the mouth of a small embayment (0.67 km).
11. York side of harbor near the mouth of a small tributary (0.85 km).
12. Kittery side of harbor just upstream from the mouth of a small tributary (0.86 km).
13. Kittery side of harbor just downstream from the mouth of tributary #3 (1.07 km). A high marsh and tidal mudflat are present.
14. York side of harbor just downstream from the old bridge pilings at Beddell Crossing (1.11 km). The channel below the bridge is initially narrow, then expands to form a flat bed that contains small boulders, cobbles, and gravel, as well as mud, detritus, and limited amounts of sand. Algae grow on the gentle slopes and in the channel on rocks. This is close to the headwaters of the harbor, and fresh water flows out during low tide, resulting in very low salinities (less than 10 ppt). In the winter, the area is usually frozen.
15. York side of harbor just downstream from tributary #3 and within an embayment area (1.23 km).
16. Kittery side near the old bridge pilings at Beddell Crossing (1.3 km); a small tidal rapids flows from a high tide pool.
17. York side of harbor near the old Beddell Crossing bridge pilings (1.4 km).
18. Kittery side of harbor near the culvert at Brave Boat Harbor Road (1.57 km).
19. York side of harbor near the culvert on Brave Boat Harbor Road (1.6 km); a concrete embankment and boulders are present.
20. York side of inner harbor (1.8 km), on Payne Road just west of Brave Boat Harbor Road.
21. York side of inner harbor just beyond the culvert on Brave Boat Harbor Road (1.9 km).

Tributary #1: The main tributary on the Kittery side of Brave Boat Harbor

that delineates Cutts Island. Distances are from the mouth of Brave Boat Harbor and Swards Cove, respectively.

- 1a. Upstream from site #10 at an embayment on the north side of the tributary (0.53 and 4.2 km).
- 1b. Upstream from site #10 on Cutts Island (S side) near the first major junction (0.91 and 3.8 km); a narrow tidal channel and significant currents.
- 1c. Upstream from the first major junction on the north side (0.96 and 3.7 km); a large circular channel is present merging into high pools.
- 1d. The second major junction on the south side (1.46 and 3.5 km); a tidal channel with strong currents and contiguous salt marsh.
- 1e. An inner riverine site on the north side with a narrow channel near a branch of the second major junction (1.46 and 3.23 km).
- 1f. A narrow channel on the north side with a tributary at the end of the second major junction near Brave Boat Harbor Road (1.52 and 3.17 km).
- 1g. The third major junction (1.55 and 3.14 km); a tidal channel with strong currents falling in both directions (see text), plus contiguous salt marshes.
- 1h. The end of a small meandering channel near Brave Boat Harbor Road (1.75 and 2.94 km); a contiguous high marsh is present.
- 1i. Approximately 0.17 km from Seapoint Road (1.83 and 2.9 km); a narrow channel with strong tidal currents, plus adjacent high marsh.
- 1j. The bridge culvert on Seapoint Road; strong tidal currents, excellent rocky substratum and a fringing marsh are present (2.0 and 2.27 km).

Tributary #2: The second major tributary, and the only one located on the York side of Brave Boat Harbor. Distances (km) are from the mouth of the Harbor.

- 2a. Approximately 0.23 km upstream from site #15 off the main Harbor channel (1.5 km); a tidal channel with a contiguous high salt marsh.
- 2b. Approximately 0.47 km upstream from site #15 off the main Harbor channel (1.74 km); an upper tidal channel with fresh water discharge.

Tributary #3: The third major tributary, and the second one located on the Kittery side of Brave Boat Harbor. Distances (km) are from the mouth of the Harbor.

- 3a. Approximately 0.06 km upstream from the mouth of tributary #3 on the west side (1.26 km).
- 3b. Directly across from #3a (1.3 km) on the east side.
- 3c. Approximately 0.23 km upstream from the mouth of tributary #3 on the west side at the first major junction (1.5 km).
- 3d. The west side of tributary #3 near Brave Boat Harbor Road (1.82 km); an upper tidal channel with fresh water drainage.

Tributary #4: Chauncey Creek and contiguous salt marshes separating Gerrish and Cutts Island, Kittery. Distances (km) from Swards Cove.

- 4a. At the junction of Seapoint Road and the bridge crossing Chauncey Creek to Gerrish Island (2.4 km); a shady, narrow channel, with scattered boulders.

- 4b. Approximately 0.15 km east of Seapoint Road bridge, near an old retaining wall or dam (2.48 km); strong tidal currents and contiguous mudflats and fringing marshes.
- 4c. A transition from a broad tidal mudflat to a narrow channel; this is a mudflat with scattered pebbles and a contiguous salt marsh (3.2 km).
- 4d. Near an oxbow and a major tidal junction (3.5 km); a narrow vertical channel with contiguous high marshes is present here.
- 4e. At the end of the northernmost tidal channel east of site #4d (4.0 km); a narrow vertical channel with contiguous high marshes.
- 4f. At the end of the southernmost tidal channel east of site #4d (3.9 km); a vertical tidal channel with a contiguous upper salt marsh.
- 4g. A inner salt marsh located behind a conspicuous coastal berm near Seapoint Beach, just east of site #4e (4.21 km).

CONSERVATION STATUS OF SAINT JOHN RIVER VALLEY HARDWOOD FOREST IN WESTERN NEW BRUNSWICK

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ABSTRACT. Saint John River Valley Hardwood Forest (SJRHF) is a regionally threatened northern disjunct plant assemblage of the central St. John River Valley and associated tributaries of southwestern New Brunswick and northeastern Maine. Two centuries of land clearance have reduced this assemblage to less than 1% of its original extent. Remaining stands, especially of more mature trees, support 31 regionally rare vascular plant taxa and are at risk due to increased cutting. Assessment of the effect of recent disturbance on SJRHF has been hampered by limited distributional information; past surveys were wide-ranging but nonsystematic. This study describes results of a systematic habitat-based survey for SJRHF remnants across 2000 km² of western New Brunswick. One hundred and twenty one stands were assessed for the presence of rare vascular plant taxa and disturbance. Fifty-four previously unknown stations with one or more rare SJRHF taxa were identified. Two new taxa were discovered for the province and one provincially extirpated taxon was re-located. One hundred and fifteen of 121 stands showed evidence of tree harvest. Within the last two decades, 46% of the surveyed sites had been fully or partially clearcut or converted to potato fields. Ongoing stand loss suggests that conservation measures are required to maintain remnant assemblages. In situations where reserve formation is not possible, occurrence of SJRHF herbs, including rare taxa, in previously select-cut stands indicates that modified low-intensity harvest strategies may not be incompatible with their persistence.

Key Words: Saint John River Valley Hardwood Forest, New Brunswick, Maine, deciduous forest, rare vascular plant taxa, conservation

Saint John River Valley Hardwood Forest (SJRHF) is a regionally threatened northern disjunct deciduous forest assemblage of the central St. John River Valley and associated tributaries of southwestern New Brunswick and eastern Aroostook County, Maine (Figure 1). The floral composition of SJRHF resembles broadleaf forests of north-central New England, eastern Ontario, and the central St. Lawrence River Valley of Quebec, but the

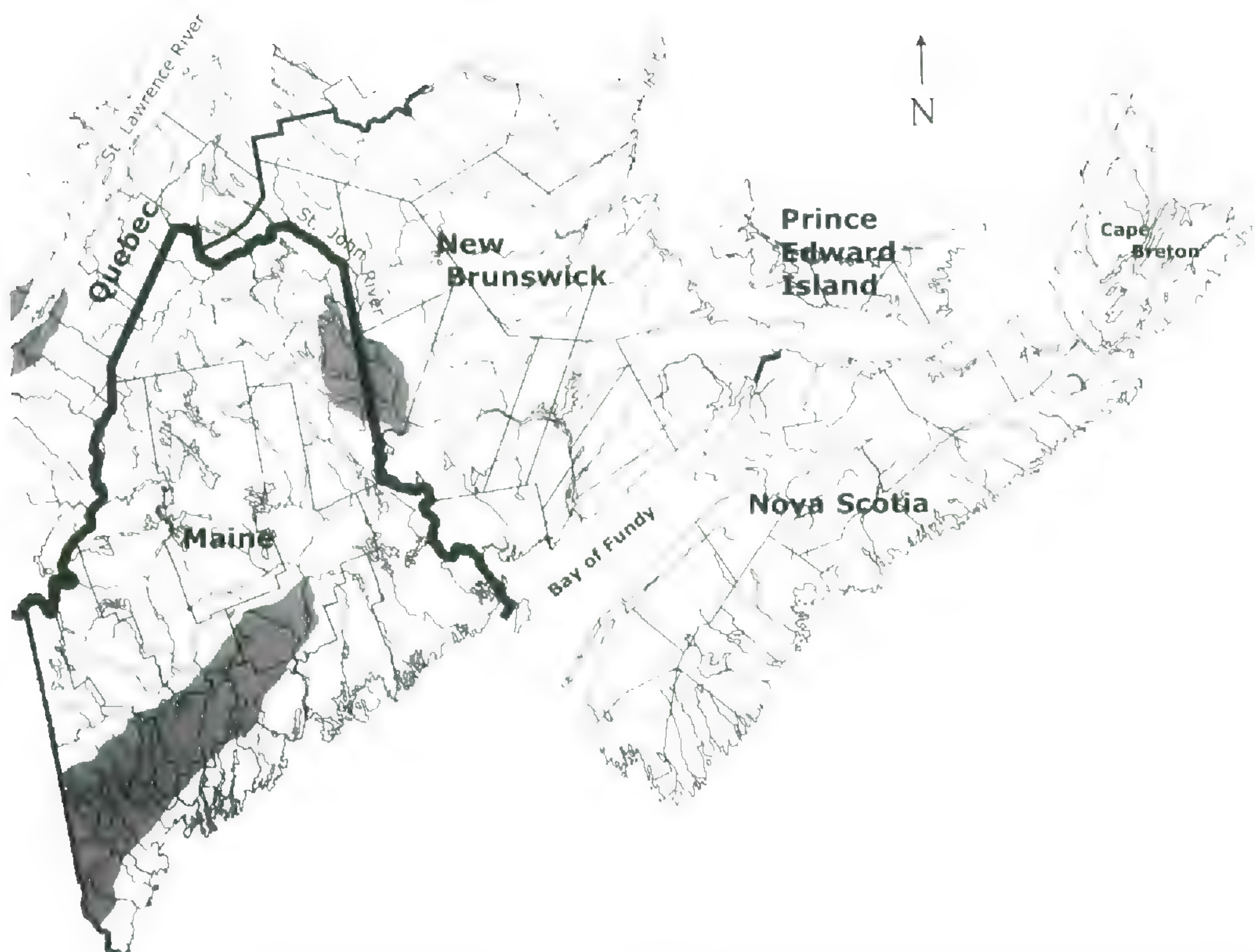


Figure 1. Major concentrations of eastern deciduous forest vascular flora (shaded) within Maine, southeastern Quebec, and the Maritime Provinces of eastern Canada. Maine and Quebec distributions extrapolated from Eastman (1981) and McMahon (1990), and from Rousseau (1974), respectively.

assemblage is isolated from these areas by 150 km or more. Associated with the enriched calcareous soils and moderate climate of the central St. John River Valley, SJRHF has been subject to extensive land clearance since the onset of European settlement in the early 1800s. Saint John River Valley Hardwood Forest presently covers less than 1% of the land base believed to have once supported this assemblage (MacDougall and Loo 1998). It provides habitat for 31 vascular plant taxa considered rare or threatened within New Brunswick, Maine, the Maritime Provinces, or the Gulf of St. Lawrence region in general (Gawler et al. 1996; Hinds 1983; New Brunswick Committee on Endangered Species 1995; Pronych and Wilson 1993). Recent increased logging and agricultural land clearance have led to concerns regarding the persistence of SJRHF in New Brunswick, though assessment of the distribution and conservation status of remnant patches has been limited by nonsystematic past survey efforts. Of particular concern are the ranges of rare SJRHF vascular plant

species, and the degree to which increased disturbance has affected SJRHF remnants.

This paper presents results of a systematic habitat-based survey for SJRHF stands across approximately 2000 km² of southwestern New Brunswick. The objectives are to: 1) describe the distribution of remnant SJRHF stands, 2) describe the rare vascular plant species composition and disturbance history of the remnants, and 3) discuss the implications of these findings for future conservation management efforts.

STUDY AREA

General description. Saint John River Valley Hardwood Forest is a deciduous forest assemblage dominated by *Acer saccharum* Marsh, *Fagus grandifolia* Ehrh., *Fraxinus americana* L., and *Betula alleghaniensis* Britton, with *Ostrya virginiana* (P. Mill.) K. Koch, *Juglans cinerea* L., *Tilia americana* L., *Ulmus americana* L., and *Tsuga canadensis* (L.) Carriere as secondary components (MacDougall and Loo 1998). This assemblage occurs near the periphery of the eastern deciduous forest formation described by Braun (1950) and possesses the most northeasterly occurring concentration of southern-affinity vascular plant taxa within this formation. It is also found along a gradient of declining deciduous forest floral diversity that runs to the north and east of North America. This is made evident by the absence of taxa such as *Carya ovata* (P. Mill.) K. Koch, *Dicentra canadensis*, and *Phegopteris hexagonoptera* (Michx.) Fee that are characteristic of broadleaf forests to the south, and which extend into Ontario and Quebec. The relative abundance of *F. americana*, plus the presence of *J. cinerea*, *T. americana*, and understory species such as *Galearis spectabilis* and *Phryma leptostachya* distinguishes SJRHF from other hardwood forest types found in northern Maine and the Maritime Provinces [Note: The butternut bark canker (*Sirococcus clavigignenti-juglandacearum*) has yet to seriously affect New Brunswick *J. cinerea* populations, though several possibly infected trees were observed in the central St. John River Valley in 1997–98 (K. Harrison, Canadian Forest Service, pers. comm.)].

Environmental conditions of the central St. John River Valley. Saint John River Valley Hardwood Forest is associated with

the rich and well-drained calcareous soils and relatively moderate climate that characterize the central St. John River Valley and associated tributary valleys. The extent of the calcareous soils generally defines the regional boundaries across New Brunswick and Maine (McMahon 1990; New Brunswick Department of Natural Resources and Energy 1996). In New Brunswick, two edaphic units predominate, and are the most fertile and intensively farmed soils in the province (Colpitts et al. 1995; New Brunswick Department of Natural Resources and Energy 1996). The Caribou Soil Unit is a finely textured and fast-draining glacial till derived from Ordovician argillaceous parent material. It is the richer of the two soil groups and occurs mostly to the west of the St. John River extending into Maine. The Carleton Soil Unit is a fine-textured compact glacial till derived from Silurian calcareous sandstone and is found on the lower reaches of the central St. John River Valley, especially on the east side of the river between Hartland and Florenceville, New Brunswick.

Topographically, the region is dissected by the Kintore Hills, a narrow, rugged, noncalcareous upland that cuts across the St. John River Valley in an east-west direction just below the juncture of the Aroostook and St. John Rivers (Figure 2). To the south of the Kintore Hills, the terrain is flat to gently rolling with elevations generally below 200 m. Upriver, the terrain is more undulating; areas below 200 m occur mostly in proximity to the Aroostook and St. John Rivers. To the east and the southeast of the central St. John River Valley, the regional boundaries are defined by noncalcareous metamorphic or granitic uplands (Loucks 1961; New Brunswick Department of Natural Resources and Energy 1996).

The climate of the central St. John River Valley is warmer and drier than adjacent regions of Maine and New Brunswick (Deevy 1951; McMahon 1990), with slightly higher average summer temperatures (Millette and Langmaid 1964), a longer frost-free period (80 to 120 days; Hinds 1980), and annual precipitation around 1050 mm (New Brunswick Department of Natural Resources and Energy 1996).

Post-glacial origins. The origins of SJRHF lie in the vegetation changes that occurred in northeastern North America following glacial retreat approximately 13,000 YBP. Saint John River Valley Hardwood Forest is assumed to be a relic disjunct as-

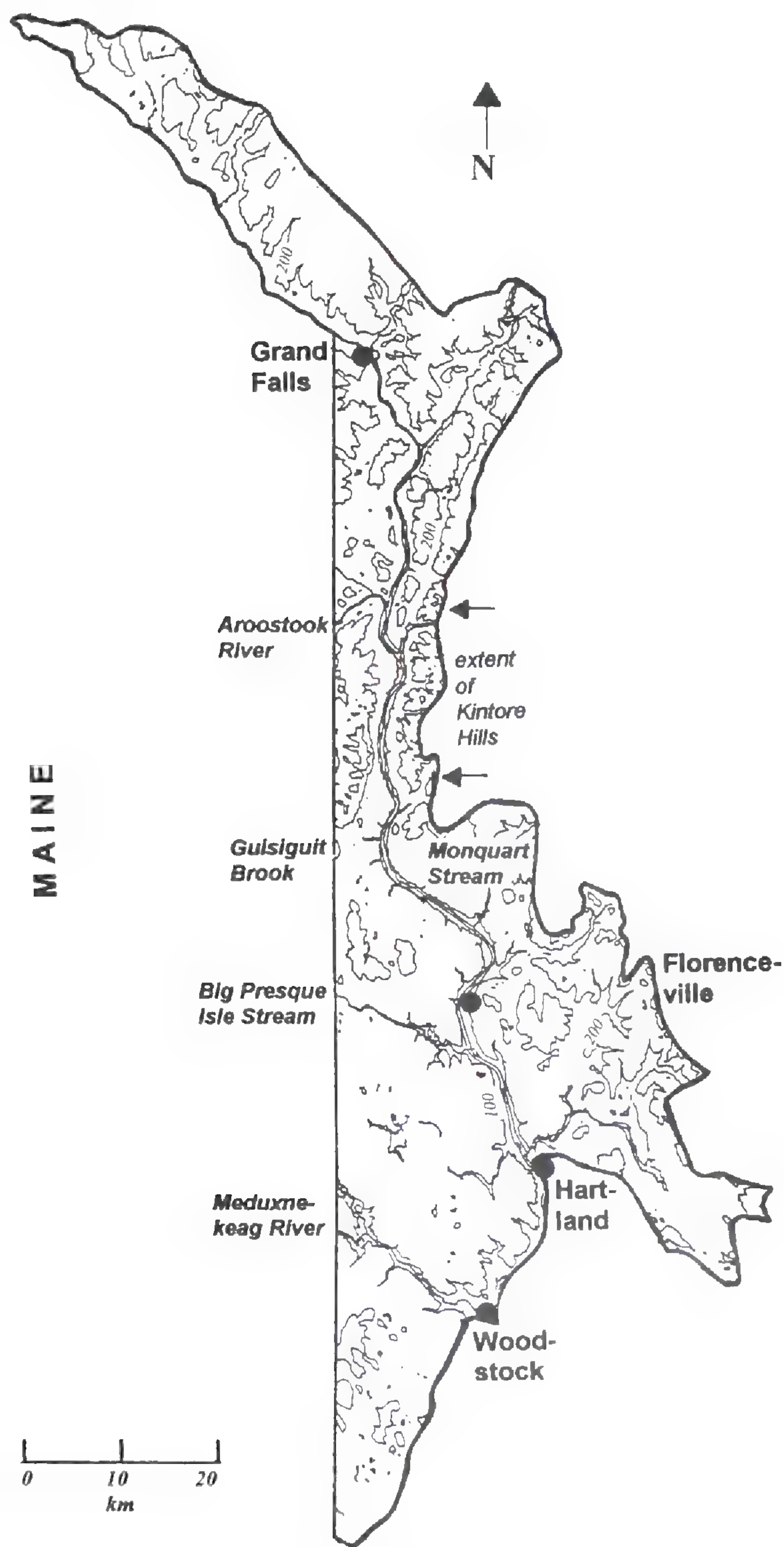


Figure 2. Study area boundaries within the central St. John River Valley of New Brunswick, as defined by New Brunswick Department of Natural Resources and Energy (1996). Contour intervals are 100 m.

semblage (*sensu* Kellman 1980; Raup 1937), a remnant of a previously wide-ranging broadleaf forest that retreated south from the Maritime Provinces due to climatic change, but was locally maintained due to favorable habitat conditions. Supporting evidence comes from two sources: tree pollen data and extrapolations of past distribution based on existing herb taxa occurrence patterns, including extirpation information.

Tree pollen data indicate that thermophilous hardwood forest was previously more abundant in northern New England and the Maritime Provinces, peaking between approximately 5100–3000 YBP (Anderson et al. 1986; Green 1987; Mott 1975a, 1975b). The northward movement of broadleaf forest was driven by the warmer and mostly drier climate that characterized northeastern North America during the early and mid-Holocene (Davis 1976; Davis et al. 1980; Prentice et al. 1991). Mott (1975a, 1975b) speculated that, at the time of peak abundance, New Brunswick's hardwood forest resembled present-day SJRHF, with high levels of *Fraxinus*, *Acer*, *Betula*, *Fagus*, and *Ulmus*. Following 3000 YBP, climatic degradation led to a decline of broadleaf tree species and an increase in *Picea* spp. and *Abies balsamea* (L.) P. Mill.

Present-day occurrence patterns of mesic herbs in the Maritime Provinces suggest that many were once more widely distributed. Isolated stations of southern-affinity herbs are scattered across the region—SJRHF is the most extensive and species-rich, but sites with some SJRHF elements also occur in northern New Brunswick's Restigouche River Valley (Cooney 1832; Hay 1896; Hinds 1983, 1986), the lower St. John River Valley of New Brunswick (Hinds 1983, 1986; MacDougall et al. 1998), and several areas in Nova Scotia including Cape Breton (Fernald 1921, 1922; Nicholls 1918; Pronych and Wilson 1993; Robinson 1903; Zinck 1998). Because many broadleaf forest herbs are notoriously poor dispersers (Bierzychudek 1982; Cain et al. 1998; Matlack 1994), formation of these isolates by long-distance migration seems unlikely: the distances separating isolates are too great, the numbers of taxa in these areas are too large to have been established by low frequency long-distance dispersal events, and the areas are separated by nondeciduous forest habitat within which mesic herbs rarely or never establish. Instead, species likely migrated into the region in association with the more widely ranging deciduous forest of the mid-Holocene. As this forest contracted,

mesic herb populations persisted in local areas with rich soils, either narrow alluvial bottomlands or sites with calcareous parent material. One area in the Maritime Provinces with few SJRHF taxa is Prince Edward Island. Prince Edward Island became isolated from the New Brunswick and Nova Scotia mainland between 5000–3000 YBP due to ocean level increase (Bousfield and Thomas 1975; Kranck 1972). Many northward-migrating plants may not have reached the Northumberland Strait area until after the corridor became submerged, though the intense level of habitat conversion on Prince Edward Island that followed settlement (Erskine 1985) could also explain floral impoverishment.

Extirpation evidence also suggests that mesic herbs were previously more prevalent. *Cryptotaenia canadensis*, a deciduous forest species found throughout most of central and eastern North America (Fernald 1950), was formerly known from several stations in New Brunswick and Maine but has not been seen in either jurisdiction since the early- to mid-1900s (Eastman 1981; Hinds 1983). Similarly, *Trillium grandiflorum* (Michx.) Salisb. has not been seen in Maine since 1926 (Campbell et al. 1995), and an old report apparently exists for western New Brunswick (H. Hinds, pers. comm.). There are also reports of *Betula lenta* L. (Braun 1950; Cooney 1832; Halliday 1937; Perley 1847), *Carpinus caroliniana* Walter (Fernow et al. 1912; Michaux 1808; Perley 1847; Speck and Dexter 1952), and *Ulmus rubra* Muhl. (Perley 1847; Speck and Dexter 1952) in the central St. John Valley or the Maritime Provinces in general, though none has ever been formally collected. Although these records could easily be the result of identification errors or misapplication of common names (e.g., “black birch”, the common name of *Betula lenta*, was often used to describe *B. alleghaniensis* in 18th century New Brunswick survey records; Lutz 1997), their occurrence is plausible due to the close proximity of their present-day northern range limits in central or southern Maine (Burns and Honkala 1990). The anecdotal nature of this extirpation evidence could reflect, in part, the period when these species disappeared from the region. Fertile habitats were usually subject to immediate clearing by settlers. Taxa that were already rare at the time of settlement may have been eliminated before botanical surveys commenced in the mid- to late-1800s.

Settlement history. The settlement of western New Bruns-

wick and eastern Aroostook County by Europeans did not begin until the early 1800s. Before this time, the Malecite Indians occupied the St. John River Valley for at least two millennia, using the river and associated tributaries as travel corridors to access coastal wintering areas and interior hunting grounds (Ganong 1899). The Malecite established few permanent settlements and practiced agriculture on a very limited basis compared to groups in central New England (e.g., Cronon 1983), and thus are believed to have had little impact on the forest.

In the early 19th century, large numbers of settlers began entering the central St. John River Valley from the lower St. John River Valley and from central Maine; land grants along the river and in the backcountry were quickly filled. At that time, the region was called “the garden of Maine” due to its fertile soils (Bailey 1894). It was estimated that it took only 50 years, ending in the 1860s, for the area to be converted from “dark wilderness” to a pastoral landscape (Bailey 1894). During the period of peak settlement, which lasted for most of the 19th century, the area was dominated by farms and small communities. Patches of forest persisted mostly as woodlots subject to selective cutting and may have served as the only refuges for SJRHF flora.

Following the turn of the century, rural land abandonment began in the central St. John River Valley, mirroring trends observed elsewhere in eastern North America as populations shifted to urban centers (Foster et al. 1998; Matlack 1997). Many farms, especially away from the rivers, reverted back to forest. Remnant SJRHF stands that survived the 1800s are thought to have remained stable for most of the 20th century. Recent increases in the demand for hardwood, combined with improved harvest capabilities, have led to increased cutting. Given that many of the region’s second growth forests have not fully developed and possess low percentages of tolerant hardwood tree species, it is the older stands supporting remnant SJRHF species that are most at risk.

Early botanical explorations and forest classifications. The botanical significance of the St. John River Valley and associated tributaries was recognized soon after settlement. In addition to the hardwood flora, botanists were also drawn to the calcareous fens, poorly drained *Thuja occidentalis* L. forests, and rocky calcareous shorelines of the region that hosted numer-

ous rare taxa [e.g., *Astragalus alpinus* L. var. *brunetianus* Fernald and *Polygala senega* L. along shorelines; *Carex sterilis* Willd., *Salix candida* Willd., and *Valeriana uliginosa* (Torr. & Gray) Rydb. in fens and swamp forest]. George Goodale, curator of botany for the Portland Society of Natural History, visited eastern Aroostook County in the 1860s. He noted the presence of southern-affinity taxa and commented on the unique character of the region relative to New England in general (Goodale 1861, 1862). During the next several decades, numerous botanical forays were made on both sides of the border, expanding the list of species and confirming the significance of the area (e.g., Fernald and Wiegand 1910; Hay 1883; St. John 1929). Species lists compiled during this period for New Brunswick (Fowler 1885; Hay 1901; Hay et al. 1882, 1884) contain most of the SJRHF taxa found today. These lists have served as valuable references for re-locating populations of rare species and assessing distribution changes.

The significance of SJRHF was also recognized in regional vegetation classifications for New England and the Maritime Provinces. Though small in area and disjunct in distribution, SJRHF was classified by Hawley and Hawes (1912) as part of the northern hardwood association typical of southern Maine, New Hampshire, Vermont, western Massachusetts, and northern New York. Braun (1950) followed this classification. Loucks (1961) similarly recognized the distinct character of this forest relative to surrounding areas, distinguishing it as a separate forest region for the Maritime Provinces.

MATERIALS AND METHODS

Identification of potential sites. Potential SJRHF sites in western New Brunswick were identified using a fine-scale habitat-based search procedure conducted on a Geographical Information System (GIS). The procedure focused on the selection of locations with a high probability of hosting rare vascular flora. Sites identified by the GIS method possessed a combination of spatially referenced environmental data layers (e.g., forest cover, soil fertility) that together best described the habitat conditions associated with SJRHF rarities: mature deciduous forest stands on well-drained calcareous soils. This habitat description was based on existing SJRHF occurrence observations in New Brunswick,

combined with studies in eastern North America that demonstrated a paucity of woodland herbs in immature and heavily disturbed deciduous forest stands (Matlack 1994; Meier et al. 1995; Whitney and Foster 1988). The use of this site identification procedure was necessary due to the extensive area of the river valley (2000 km²) and the random and visually indiscrete distribution of mature stands embedded within a landscape of farms, settlements, and regenerating forest. By directing ground surveys to mature deciduous forest stands, large areas considered unsuitable for rare SJRHF vascular flora in terms of habitat (e.g., bogs) or disturbance (e.g., old field *Populus* spp.–*Abies balsamea* forest) were avoided. Site identification was not conducted in Maine due to time constraints and the perception that the hardwood forests of Aroostook County had undergone more intensive and widespread disturbance than in New Brunswick (S. Rooney, pers. comm.). Only a few scattered SJRHF stations are known from Aroostook County, and they contain just over half of the rare taxa found in New Brunswick.

The GIS search method for identifying potential sites consisted of three sequential steps. The first two steps—identifying the regional study area boundary and selecting well-drained calcareous soil units—employed a previously established multi-level Ecological Land Classification (ELC) developed for the province of New Brunswick (New Brunswick Department of Natural Resources and Energy 1996; Zelazny et al. 1997). The ELC was derived using combinations of abiotic and vegetational data layers across a range of spatial resolutions, including fine-scale edaphic and topographic habitat variables targeted by this study. The third step in the identification process involved stand-level photo-interpreted data describing canopy composition and age class.

The study area boundary was defined by the ELC district-level (1:250,000) classification delineated using geomorphological and topographical information. This boundary followed the distribution of calcareous parent material within the St. John River Valley, running from below Woodstock, New Brunswick, to St. Leonard, New Brunswick, north of Grand Falls (Figure 2). The international boundary defined the western limit. All previously known SJRHF sites but one occurred in this district.

The second step employed ELC site-level (1:20,000) designations delineated using information on soil fertility, soil drainage, elevation, and slope, and supplemented with forest cover data.

Site units with well-drained and calcareous-based soils on all slope and elevation classes were selected. These units covered 51% of the entire district within the central St. John River Valley; the remaining area included poorly drained calcareous wetlands, mostly dominated by *Thuja occidentalis* forest, and noncalcareous sites of the Kintore Hills. All previously known SJRHF sites were found on the selected units.

The final step involved stand-level, photo-interpreted forest cover data. These data, described by New Brunswick Department of Natural Resources and Energy from 1981 photos (1:12,500 resolution), identified dominant canopy composition and age-class in forest stands. Stands were selected for “100% tolerant hardwood” of the “mature” (> 80 years) and “overmature” (> 120 years) age classes occurring on the three targeted site-level units. Seven of the 15 previously known SJRHF sites were not captured by this procedure; all had been classified from aerial photographs as “100% tolerant hardwood”, but in the “immature” age class (50–80 years). This suggested that these sites were either incorrectly classified “mature” stands, or that the assumption that rare SJRHF plant assemblages only occurred in older growth stands was incorrect.

The end product of this GIS-based search, incorporating the three data layers and covering all of New Brunswick’s central St. John River Valley, was 108 small (mean = 11.3 ha; range 0.82–112.3 ha) and isolated stands covering 0.8% of the study region. They were the basis for all initial field work.

Field assessment. The GIS-identified stands, plus the previously known SJRHF sites not captured by the procedure, were surveyed by either one of two field crews between May 21–July 1, 1997. This period was selected as the optimal time for viewing spring ephemeral plant taxa in New Brunswick. The survey procedure focused on the location and abundance of targeted rare vascular plant taxa (Table 1). Targeted flora were SJRHF taxa listed as provincially uncommon, rare, or very rare by Hinds (1983, 1986), plus deciduous forest taxa known from north-central and northern Maine (*Dicentra canadensis* and *Panax quinquefolius*, respectively) but not recorded in New Brunswick.

Each stand was surveyed to: 1) generally characterize tree and understory plant composition and 2) locate rare vascular plants. Formal transect and plot sampling were not conducted due to

Table 1. Rare vascular plant taxa of Saint John River Valley Hardwood Forest. X = uncommon, rare, or very rare in New Brunswick (NB; Hinds 1983, 1986), rare or very rare in Maine (Haines and Vining 1998), rare in Nova Scotia (NS; Pronych and Wilson 1993; Zinck 1998). – = does not occur in the province; ** = occurred historically; may be extirpated; + = not listed as rare. “Prev.” is the number of records previously known from New Brunswick (Connell Memorial Herbarium UNB). “New” is the number of new records found by this study. Nomenclature follows Campbell et al. 1995. # = possibly extirpated from Prince Edward Island (Erskine 1985); ## = rare in Prince Edward Island (Erskine 1985).

Taxon	Status				
	NB	Maine	NS	Prev.	New
<i>Adiantum pedatum</i> L. #	X	+	X	9	19
<i>Allium tricoccum</i> Aiton	X	X	X	9	0
<i>Asarum canadense</i> L.	X	X	–	15	21
<i>Botrychium lanceolatum</i> (S. G. Gmel.) Angstr. subsp. <i>angustisegmentum</i> Pease & A. H. Moore	X	+	X	7	2
<i>Cardamine concatenata</i> (Michx.) Sw.	X	X	–	3	1
<i>Carex cephaloidea</i> (Dewey) Dewey	X	+	–	2	1
<i>Carex hirtifolia</i> Mack.	X	X	+	4	2
<i>Carex plantaginea</i> Lam.	X	+	**	6	12
<i>Carex sprengelii</i> Dewey ex Spreng.	X	X	–	9	2
<i>Caulophyllum thalictroides</i> (L.) Michx.	X	+	X	13	9
<i>Cryptotaenia canadensis</i> (L.) DC.	**	**	–	–	0
<i>Cynoglossum virginianum</i> L. var. <i>boreale</i> (Fernald) Cooperrider	X	X	X	3	1
<i>Cypripedium pubescens</i> Willd. ##	X	+	X	29	20
<i>Desmodium glutinosum</i> (Muhl. ex Willd.) A. Wood	X	+	X	–	1
<i>Dicentra canadensis</i> (Goldie) Walp.	–	X	–	0	0
<i>Dirca palustris</i> L.	X	+	X	6	7
<i>Dryopteris clintoniana</i> (D. C. Eat.) Dowell	X	X	–	1	1
<i>Dryopteris goldiana</i> (Hooker ex Goldie) A. Gray	X	X	–	5	13
<i>Dryopteris clintoniana</i> × <i>goldiana</i>	X?	X?	–	0	1
<i>Dryopteris</i> × <i>dowellii</i> (Farwell) Wherry	X?	X?	–	0	1
<i>Elymus hystrix</i> L.	X	X	X	3	1
<i>Festuca subverticillata</i> (Pers.) E. B. Alex- eev	X	X	X	2	4
<i>Galearis spectabilis</i> (L.) Raf.	X	X	–	7	4
<i>Hepatica nobilis</i> P. Mill. var. <i>obtusa</i> (Pursh) Steyerm.	X	+	X	11	1
<i>Impatiens pallida</i> Nutt.	X	X	+	2	0
<i>Panax quinquefolius</i> L.	–	X	–	0	0
<i>Phryma leptostachya</i> L.	X	**	–	8	7
<i>Rubus occidentalis</i> L.	X	+	–	8	8

Table 1. Continued.

Taxon	Status				
	NB	Maine	NS	Prev.	New
<i>Sanicula odorata</i> (Raf.) Pryer & Phillippe	X	X	+	4	1
<i>Sanicula trifoliata</i> E. P. Bicknell	X	X	–	3	3
<i>Triosteum aurantiacum</i> E. P. Bicknell	X	X	X	6	1
<i>Viola canadensis</i> L.	X	X	X	4	3

their potential insensitivity to rare plant distribution (H. Hinds, pers. comm.). Instead, stands were first walked in their entirety; all encountered tree and understory species were recorded and estimated for stand abundance. Aerial photographs assisted in determining stand boundaries and in locating stream depressions and disturbance features (e.g., old trails, sharp changes in canopy architecture) not readily apparent from the ground. Once the stand had been walked, search effort focused on habitat features specifically associated with the presence of rare SJRHF taxa, especially groundwater seepage zones, micro-topographical depressions, exposed limestone outcrops, and stream-side alluvial formations. Epiphytic moss and liverwort taxa were informally surveyed in 53 stands [B. Bagnell (B & B Botanical, St. John, New Brunswick), unpubl.], representing the most widespread survey of the bryophyte flora for this region of New Brunswick. Disturbance history was assessed based on the presence of old roads and trails, stumps, fences, or stone piles within the stand, plus evidence of recent disturbance subsequent to the 1981 aerial photos. Stand structure was informally described to corroborate the photo-interpreted age class designations (e.g., did a “mature” stand possess small and uniformly sized trees more characteristic of young regenerating stands?). After July 1, some of the earliest surveyed sites were revisited to search for late-emerging species (e.g., *Impatiens pallida*).

Results from the initial survey period indicated that the Meduxnekeag River watershed possessed the greatest concentration of SJRHF sites with the most diverse floral assemblages compared to all other areas. In addition, all seven previously known SJRHF sites identified as “immature” occurred in this watershed. To determine if other stands classified as “immature” hosted rare assemblages in this area, the GIS-site identification procedure was used again. Additional stands were selected using stand size (>

10 ha), canopy composition (“100% tolerant hardwood”), and age class (“immature”) on well-drained calcareous site units. Six sites were identified and surveyed.

RESULTS

One hundred and twenty one sites were surveyed within New Brunswick’s central St. John River Valley, combining GIS-identified sites with previously known sites and additional stands identified within the Meduxnekeag River watershed. Four stands were not assessed due to incorrect photo-interpretation of stand composition (i.e., not “tolerant hardwood”). Access to three stands was denied by the land owner.

Forty-nine percent of the previously unsurveyed sites, including the six Meduxnekeag River sites, were considered to be SJRHF stands. An SJRHF stand was defined as a tolerant hardwood-dominated forest with a species-rich herb community that included one or more rare vascular plant taxa. This definition distinguished SJRHF from GIS-identified tolerant hardwood stands that lacked both common and rare SJRHF herb taxa due to disturbance, and from GIS-identified stands that were obviously mature but lacked SJRHF herb taxa due to site conditions. This latter distinction applied mostly to hardwood stands in the north where climate apparently limits SJRHF floral establishment.

Within the surveyed SJRHF stands, each targeted taxon was observed at least once except *Impatiens pallida* (Table 1). The most frequently observed rare species were *Asarum canadense* (21 new stations), *Cypripedium pubescens* (20 new stations), *Adiantum pedatum* (19 new stations), *Dryopteris goldiana* (13 new stations), *Carex plantaginea* (12 new stations), and *Caulophyllum thalictroides* (9 new stations). Several taxa were very infrequent, occurring in a small number of stands with populations typically fewer than 10 individuals (*Galearis spectabilis*, *Sanicula odorata*, *Dryopteris clintoniana*, *Cardamine concatenata*). Two fern hybrids, *D. × dowellii* and *D. clintoniana × goldiana* were recorded (J. Goltz) for the first time in the province. *Desmodium glutinosum*, not seen in New Brunswick since 1899 and classified as extirpated (New Brunswick Committee on Endangered Species 1995), was rediscovered on a calcareous shoreline (G. Bishop and B. Bagnell) immediately adjacent to a stand on the Meduxnekeag River.

Distribution of targeted SJRHF flora was concentrated in the southern half of the central St. John River Valley between Woodstock and Florenceville. The Meduxnekeag River Valley contained the largest number of stations (15) with one or more populations of all targeted rare taxa that were observed. Other watersheds of significance were Guisguet Brook (ten stations) and Big Presque Isle Stream (six stations). Monquart Stream (seven stations) was the only watershed on the east side of the St. John River with multiple stations. To the north, the abundance and diversity of SJRHF taxa quickly diminished. *Tilia americana* was not recorded upriver from Hartland, New Brunswick. Most taxa reached their northern limit at the downriver edge of the Kintore Hills. North of this upland formation, only six rare taxa were observed; three of these were limited to one station. At Grand Falls, near the northern extent of the study area, most SJRHF species no longer occurred, including *Fraxinus americana* and *Ostrya virginiana*. To the south, downriver from Woodstock, surveyed stands were also less diverse; only four rare taxa were recorded.

A sharp contrast in the within-stand distribution of SJRHF ground flora was observed between seep and non-seep areas. Rare flora were usually clustered in moist microsites, even if these features covered only a small percentage of the total stand area. Dominant seep flora included combinations of *Deparia acrostichoides* (Sw.) M. Kato, *Matteuccia struthiopteris* (L.) Todaro var. *pennsylvanica* (Willd.) Morton, *Adiantum pedatum*, and occasional *Dryopteris goldiana*, with *Erythronium americanum* Ker Gawl., *Viola pubescens* Aiton, *Sanguinaria canadensis* L., *Asarum canadense*, and *Arisaema triphyllum* (L.) Schott prevalent. *Juglans cinerea* and *Tilia americana* occurred primarily in these areas. In non-seep areas, dominant ground flora were *E. americanum*, *Maianthemum racemosa* (L.) Link, *Claytonia caroliniana* Michx., *Polystichum acrostichoides* (Michx.) Schott, *Trillium erectum* L., *Botrychium virginianum* (L.) Sw., and *Dicentra cucullaria* (L.) Bernh. Large patches of *Taxus canadensis* Marshall were occasionally present.

One hundred and fifteen of the 121 surveyed stands showed direct evidence of human disturbance based on the presence of stumps, old extraction trails, or stone fences. At ten of these sites, the overstory had been completely removed since 1981 and the stands converted either to potato fields or clearcut; these were excluded from further analysis. Of the remaining stands, 73 of

111 showed evidence of logging within the last 16 years; 37% had been partially harvested. Three stands contained rock walls or split-rail fences within their understory, indicating that part of the stand had formerly been cultivated or pastured. No area of forest understory showing signs of past cultivation or pasturing possessed any rare floral elements.

DISCUSSION

Distribution patterns. Saint John River Hardwood Forest stands were found to be more numerous than originally thought but, unexpectedly, they did not occur throughout the study area. Stand distribution was concentrated below the Kintore Hill formation between Woodstock and Florenceville. Upriver, most vascular plant taxa became increasingly infrequent, or were absent, despite the persistence of the rich soils. The most likely primary cause of this decline is climate, which presumably becomes cooler to the north due in part to increased elevation. Greater upriver topographical undulation may also be a factor. Seepage zones that support rare taxa are less likely to form on steep slopes, occurring instead on the lower slopes and bottomlands where the farms, settlements, and roads of this area are concentrated. In addition, the Kintore Hills may act as a geographic barrier to upriver migration, as these noncalcareous hills rise sharply from the edge of the St. John River and prevent bottomland formation. To the south, in the lower St. John River Valley, the absence of calcareous parent material is thought to explain the reduced presence of SJRHF vascular flora, especially the rare taxa, though longer-term human disturbance, dating back to the early 1700s, and substantial flooding by a hydroelectric dam above Fredericton (est. 1968) undoubtedly restrict present-day occurrence as well.

Within-stand floral surveys indicated that rare SJRHF vascular plant taxa were skewed towards moist microsites. The processes driving this distribution pattern are unclear. It may reflect higher moisture levels, though the accumulation of ground water and surface runoff may also concentrate solubilized mineral nutrients at these locations. The prevalence of *Juglans cinerea* and *Tilia americana* in seeps may indicate that vernal understory light intensity is also a factor (e.g., Brewer 1980), as both leaf-out several weeks later than the other deciduous tree species.

Predictive success. The habitat-based search method, driven largely by Ecological Land Classification data, had a success rate of 49% for sites with one or more rare species. This level of predictive success in finding new rare plant stations is considerably higher than that of other studies using similar methods (e.g., 18% by Stahle and Chaney 1994; 10% by Sperduto and Congalton 1996; 4% by Nekola 1994), likely reflecting the strong association between the selected habitat features and the occurrence of SJRHF floral elements. Previous survey limitations may have also contributed to the high success. Given that most sites with rare flora were on the west side of the St. John River Valley, this procedure should also be attempted in Maine (two sites abutted the international boundary). Even if the deciduous forests of Aroostook County have been more intensively disturbed, these results demonstrate that very small and highly isolated stands can contain rare SJRHF elements.

Conservation implications. One of the underlying assumptions of this study was that stand remnants with rare SJRHF taxa would show no evidence of human disturbance. It was thought that these stands served as refuges from the perturbations affecting other forested areas, an assertion supported by the fact that rare taxa were previously unknown from the regenerating forests of the region. Results from this survey, however, revealed that this assertion was overly simplistic. Only 4% of the “mature” and “over-mature” surveyed stands lacked evidence of past selective cutting, such as stumps or old skid trails. In addition, 13 “immature” tolerant hardwood stands within the Meduxnekeag River watershed contained rare species. Although no rare SJRHF vascular plants are known from regenerating stands with coniferous and intolerant hardwood canopies (i.e., old field), the occurrence of rare herbs in previously disturbed tolerant hardwood sites implies that these taxa can withstand some stand perturbation. This is consistent with Keddy and Drummond (1996) who speculated that deciduous forest understory flora may be insensitive to certain forms of cutting. Post-harvest herb studies by Reader (1987) and Metzger and Shultz (1981) both demonstrated little deciduous forest herb loss following selective logging.

It is beyond the scope of this paper to determine the relationship between stand disturbance and herb persistence. Conclusions are limited, in part, due to the absence of comparative surveys in

“immature” deciduous stands in the region. It is unknown if “immature” stands outside of the Meduxnekeag River Valley watershed also support rare floral assemblages, or whether this is a localized phenomenon. In addition, absence of detailed stand measurements prevents determining if the photo-interpreted distinction between “mature”/“overmature” and “immature” stands is ecologically meaningful. The key feature used to distinguish “immature” stands from older ones is canopy architecture, yet differences in canopy appearance could reflect site differences rather than stand history in some cases. Also, canopy architecture may not be a true reflection of stand age if long-term selective high-grading has occurred. Persistent cutting of older trees would prevent the development of structural features typical of late-seral deciduous forest (e.g., large-sized individuals, snags and large canopy gaps created by mature tree death) but may not affect the persistence of SJRHF understory vegetation due to the continued retention of large portions of the canopy.

Despite these explanatory limitations, it is clear that present-day rare SJRHF taxa can occur in stands that have been disturbed to some degree. This raises two questions regarding the long-term conservation status of SJRHF assemblages: 1) does the occurrence of rare taxa in disturbed sites reflect post-disturbance colonization, or the persistence of pre-disturbance populations? and 2) for rare herbs that apparently tolerate some disturbance, which harvest schemes are least detrimental to their persistence?

Determining the origins of SRJHF ground flora within hardwood remnants requires testing the dispersal and establishment capabilities of these taxa. Although such information is locally unavailable, studies in deciduous forests of the eastern United States suggest that woodland herb establishment in regenerating stands is infrequent, or extremely slow on the order of centuries, due to poor dispersal ability (Duffy and Meier 1992; Matlack 1994). Post-disturbance soil fertility changes (e.g., Holmes and Zak 1999) may also be a factor. If SJRHF understory species are not re-establishing, most, if not all, of the present-day sites must be remnants of the pre-colonial forest that escaped deforestation in the 19th century and then survived subsequent stand disturbances. This implies that ongoing land clearance and clearcutting are incrementally reducing the number of SJRHF site occurrences, and that protection of the remaining areas becomes critical for SJRHF persistence within New Brunswick and Maine. Site loss

would be most detrimental to rare taxa that are currently known from only a few locations. As a result, in addition to protection, reintroduction programs may be needed for these taxa to increase the number of occurrences within the region, and to bolster within-stand populations. A demographic analysis of *Asarum canadense* (Damman and Cain 1998) suggested that populations below 25 individuals were not viable under optimal environmental conditions. If this minimum viable population level is assumed for all SJRHF species, then several may presently be at risk (*Cardamine concatenata*, *Sanicula odorata*, *Dryopteris clintoniana* and associated hybrids, and *Galearis spectabilis*).

Observations from this study suggest that there may be select-cut scenarios not detrimental to rare SJRHF flora. Unfortunately, there are insufficient data to quantify disturbance thresholds above which understory herbs are adversely affected. Presumably, the overall effect of disturbance on SJRHF species depends on the intensity, frequency, and extent of intrusions. Factors such as type of harvest (extraction by horse versus skidder), harvest season (snow cover could protect some species), extent of canopy removal, location (seepage zones), and presence of weedy invasive species in the seedbank all influence post-harvest ground flora composition. If the effect of various cutting intensities could be determined, however, it may be possible to modify management approaches so that SJRHF understory species are maintained. At sites where reserve formation is not an option due to landowner reluctance, implementing such strategies may be the only viable conservation alternative. Given the increased pressures for conversion of forests to agricultural fields within western New Brunswick, maintaining working forests may serve as an effective means of maintaining these stands in lieu of full protection.

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NEW TAXA AND NOMENCLATURAL PROPOSALS IN MISCELLANEOUS FAMILIES—UTAH AND ARIZONA

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ABSTRACT. Six new taxa from Utah and one from northern Arizona are described and one new nomenclatural proposal is presented, as follows: *Erigeron huberi* S. L. Welsh & N. D. Atwood, *sp. nov.*; *Salvia columbariae* var. *argillacea* S. L. Welsh & N. D. Atwood, *sp. nov.*; *Astragalus lentiginos* Douglas *ex* Hook. var. *trumbullensis* S. L. Welsh & N. D. Atwood, *var. nov.*; *Sphaeralcea grossulariifolia* (Hook. & Arn.) Rydb. var. *fumariensis* S. L. Welsh & N. D. Atwood, *var. nov.*; *Oenothera murdockii* S. L. Welsh & N. D. Atwood, *sp. nov.*; *Aquilegia desolaticola* S. L. Welsh & N. D. Atwood, *sp. nov.*; *A. fosteri* (S. L. Welsh) S. L. Welsh, *comb. nov.*; *A. loriae* S. L. Welsh & N. D. Atwood, *sp. nov.*

Key Words: Compositae, Labiatae, Leguminosae, Malvaceae, Onagraceae, Ranunculaceae, nomenclature, Utah, Arizona

Continued exploration of the varied and numerous habitats of Utah and northern Arizona, and further examination of herbarium specimens from those places, demonstrate the existence of seven new taxa. These have been compared not only with specimens from elsewhere in Utah and Arizona, but also with those in much of the American West. These taxa represent local entities with narrow ranges of ecological tolerance, and they are often restricted to specific geological strata or narrowly defined habitats. Admittedly, much work remains to be done. The flora, after more than 15 decades of exploration, is still imperfectly known, and potentially there are other narrowly endemic taxa to be discovered, described, and named.

COMPOSITAE

Erigeron huberi S. L. Welsh & N. D. Atwood, *sp. nov.* TYPE: U.S.A. Utah: Duchesne Co., Lake Fork Mtn., Uinta Mtns., T2N R5W S16, NW1/4 of NE1/4, Uinta Base Meridian. Plants growing along windswept ridge crest above limestone talus slopes,

rocky soils, 10,900 ft., 21 Jul 1998, *A. Huber & C. Wedig* 3825 (HOLOTYPE: BRY!; 7 isotypes to be distributed).

Similis *Erigeron untermannii* S. L. Welsh & Goodrich in aspectis generalibus sed in caudicibus simplicibus involucro brevior et radiis angustioribus differt.

Perennial pulvinate herbs with a shortly branched caudex, the caudex branches with few persistent leaves or leaf bases; leaves mainly or all basal, 0.3–2.2 cm long, 0.8–2.5 mm wide, narrowly oblanceolate to spatulate, the surfaces glabrous or with ascending hairs, ciliate (especially at the base) with hairs less than 1 mm long; cauline leaves 1 or commonly lacking; scapes (or peduncles) 1.5–2.7 cm tall; head solitary; involucre 5–10 mm wide, 3–5 mm high, the bracts more or less imbricate, green, or the inner somewhat chartaceous, the margins hyaline, the tips greenish or stramineous, rather densely villous-hispidulous with short, spreading, multicellular hairs; rays 12–30, white, violet-tinged, or violet, 3.5–7 mm long, 0.7–1 mm wide; disk corollas 2–2.3 mm long; pappus apparently single, of ca. 10 slender, fragile bristles; achenes 2-nerved, pilose.

ADDITIONAL SPECIMENS (PARATYPES): UTAH: Duchesne Co., Lake Fork Mtn., Uinta Mtns., T2N R5W S16, NW1/4 of NE1/4, Uinta Base Meridian, limestone substrate, rocky and gravelly soils, windswept ridge top above limestone talus, scattered spruce trees, 10,900 ft., 2 Jul 1998, *Huber & Wedig* 3752 (BRY!).

HABITAT AND DISTRIBUTION. *Erigeron huberi* grows on alpine ridge crests above limestone talus with scattered spruce krummholz at ca. 3325 m. It is known only from Lake Fork Mountain, Uinta Mountains, Duchesne County, Utah. The species is endemic (Figure 1).

This species seems almost certainly to be closely allied to the nearby disjunct species, *Erigeron untermannii* S. L. Welsh & Goodrich, with which it is compared in the diagnosis. That species occurs on the south rim of the Uinta Basin in Utah. In the key to the species in Cronquist's (1947) revision, the plants would key to the rare Canadian species, *E. radicans* Hook., because of their short disk corollas and few pappus bristles. From that species, disjunct by several hundred kilometers, the present taxon differs in its less complex caudex, fewer cauline leaves (0 or 1, not 2 or 3), and fewer (12–30, not 20–50) and narrower (0.7–1,

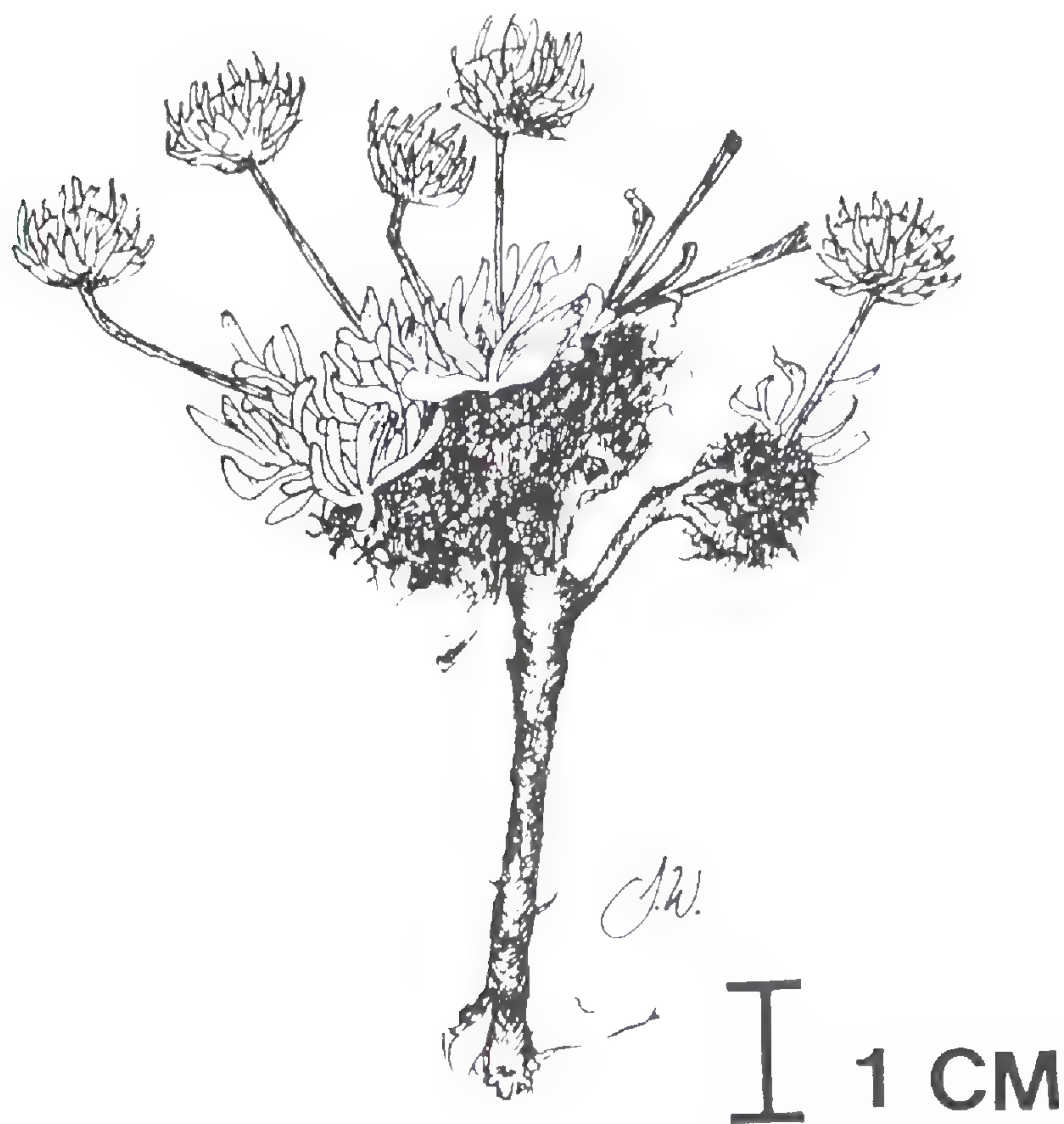


Figure 1. *Erigeron huberi* S. L. Welsh & N. D. Atwood (*Huber & Wedig* 3825 BRY).

not 1.9–2.2 mm) ligules. From *E. nanus* Nuttall, a disjunct species from southern Wyoming, Idaho, and northwestern Utah, it differs in the less complex caudex, the shorter ciliate hairs at the leaf base (less than 1, not over 1 mm), shorter involucre (3–5, not 5–8 mm), and narrower ligules (0.7–1, not 1.3–2.5 mm wide).

A closely similar collection, identified tentatively as *Erigeron radicans* by its collector (*Mosely 1526* BRY!), is known from Lemhi County, Idaho. It differs in subtle ways from both the present proposal and from *E. radicans*, i.e., in having 22–33 ligules (these 1.1–1.3 mm wide), cauline leaves consistently 1 or 2, and basal leaves 0.8–1.3 mm wide. There are, in *Mosely 1526*, other subtle differences in pubescence, that of the stem being more densely and uniformly ascending-hairy, that of the involucre being spreading-pilose.

The species is named after Alan Huber, enthusiastic collector and student of the floras of the Uinta Mountains and Uinta Basin of Utah.

LABIATAE

Salvia columbariae Benth., Labiat. Gen. Spec., fasc. 3: 302. 1833.

Annual; stems branching and leafy at the base, 1–5 dm tall, cinereous with short retrorse hairs; basal leaves 3–18 cm long, the petioles 1.5–7 cm long, the blades 2–11 cm long, oblong-ovate, pinnatifid or bipinnatifid into toothed or incised divisions; flowers in capitate verticels, these 1–3 cm wide, terminating the stems and branches; bracts suborbicular, awn-tipped, suffused with rich dark purple or merely purple; calyx ca. 1 cm long, purplish, arcuate, the middle spinose tooth of the upper lip bifid or trifid, the lobes 1.5–2.6 mm long; corolla blue; stamens with upper arm of connective linear and lacking an anther, the lower branch deflexed and with a fertile anther.

The above description is for the typical variety. The differences between it and var. *argillacea* are given in the following key and in the description of var. *argillacea*.

1. Flowers blue; floral bracts typically a rich dark purple, the median calyx teeth with bifid or less commonly trifid awns 1.5–2.6 mm long; plants of alluvial substrates at low elevations in Washington Co., Utah and widely distributed elsewhere 1a. var. *columbariae*
1. Flowers white; floral bracts green or less commonly some suffused with red purple, the median calyx teeth mainly with bifid awns 0.8–1.5 (–1.7) mm long; plants of the clays of the Chinle Formation at higher elevations in eastern Washington and central to western Kane Cos., Utah 1b. var. *argillacea*

1a. var. *columbariae*

This variety grows in creosote bush, Joshua tree, blackbrush, and pinyon-juniper communities at 800 to 1465 m in western Washington Co., Utah, and in California, Nevada, Arizona, and Mexico. The plants flower in Utah from mid-March to mid-May.

1b. var. *argillacea* S. L. Welsh & N. D. Atwood, var. nov.
TYPE: U.S.A. Utah: Kane Co., clay-silt of Chinle Formation, *Phacelia-Eriogonum-Astragalus* community, at 1700 m, Kitchen Corral Canyon, 1 mi. W of Kitchen Corral Point & 6 mi. SW of Mollies Nipple, T41S R3W S33, red-purple outcrops, sparsely

vegetated in pinyon-juniper community, 5 Jun 1993, *S. L. Welsh* 25642 (HOLOTYPE: BRY!; 9 isotypes distributed previously as *Salvia columbariae*).

Ab *Salvia columbariae* Benthām in floribus bracteis et calycibus coloris et dente calycis bifidis brevioribus absimilis.

Annual; stems branching and leafy at the base, 0.9–3.7 dm tall, cinereous with short retrorse hairs; basal leaves 3–7 cm long, the petioles 1.0–3.8 cm long, the blades 2.0–5.5 cm long, oblong-ovate, pinnatifid or bipinnatifid into toothed or incised divisions; flowers in capitate verticels 1–3 cm wide, terminating the stems and branches; bracts suborbicular, awn-tipped, green, or rarely suffused with red-purple; calyx ca. 1 cm long, green, arcuate, the middle spinose tooth of the upper lip bifid, the lobes 0.8–1.5 (–1.7) mm long, rarely shortly trifid; corolla white; stamens with upper arm of connective linear and lacking an anther, the lower branch deflexed and with a fertile anther.

ADDITIONAL SPECIMENS (PARATYPES; ALL BRY!): UTAH: Kane Co., location as for the holotype, 18 Jun 1998, *Atwood & Welsh* 23896; ditto, 4 Sep 1998, *Atwood & Welsh* 24126; Washington Co., along dirt road south of Rockville and at the west base of Smithsonian Butte, 26 May 1973, *Atwood* 5141; ditto, 6 mi. N of Hwy. 59 on the Big Plain junction road to Rockville, T42S R11W S21, Chinle Formation, 8 Jun 1976, *Atwood* 6748; ditto, T42S R11W S16, Wire Mesa just NW of Smithsonian Butte, 8 Jun 1983, *Higgins* 13641; ditto, 1 Jun 1985, *Higgins* 15579; ditto, T41S R10W S14, 6 Jun 1984, *Welsh, Higgins & Thorne* 22912; ditto, Smithsonian Butte vicinity, ca. 5 mi. SW of Rockville, T42S R11W S21, 23 May 1985, *Welsh* 23483; ditto, 14 May 1986, *Higgins* 16415; ditto, T42S R11W S14, 4 mi. SE of Rockville, 17 Jun 1987, *Thorne, Clark & Welsh* 5387; ditto, Petrified Forest, 2 mi. N of Rockville, T45S R11W S25, 11 Jun 1988, *Welsh* 24045; ditto, Parunuweap Canyon, Shunesburg, East Fork Virgin River, T42S R10W S3, 19 May 1989, *Higgins* 18203.

HABITAT AND DISTRIBUTION. *Salvia columbariae* var. *argillacea* is found growing with *Oenothera murdockii*, *Phacelia cephalotes*, *Eriogonum subreniforme*, *Molucella*, and *Astragalus ampullarius* communities on the Mesozoic Chinle Formation, in the pinyon-juniper zone at 1295 to 1700 m. It is endemic to eastern Washington County and western Kane County, Utah (Figure 2).

This white-flowered and typically green-bracteate taxon, with its shortly bifid calyx teeth, is apparently restricted ecologically to fine-textured, physiologically harsh, saline substrates of the Chinle Formation, where it grows with other peculiar plant taxa,



Figure 2. *Salvia columbariae* Benthām var. *argillacea* S. L. Welsh & N. D. Atwood (Atwood & Welsh 23896 BRY).

often but not always, on bizarre “gypsum boils,” which consist of upheaved portions of that formation. The typical, purple-bracteate and blue-flowered, *Salvia columbariae*, is a substrate generalist occurring mainly on alluvium or colluvium derived from many sources; it is not known from east of the Hurricane Cliffs in Washington County, Utah. There are specimens, which might belong to var. *argillacea*, known from the Chinle Formation in the vicinity of Quail Creek, on the southeastern flank of the Pine Valley Mountains, west of the Hurricane Cliffs. More materials of those are necessary to adequately assess their taxonomic status. There are, however, within the white-flowered populations occasional specimens whose bracts and/or calyces are tinged with red-purple. These individuals, as their white-flowered neighboring plants, have shortly bifid middle calyx teeth. The white-flowered plants have been collected from mid-May to mid-June.

LEGUMINOSAE

Astragalus lentiginosus Douglas *ex* Hook., Fl. Bor.-Amer. (Hooker) 1: 151. 1831.

Along the Grand Canyon in Northern Arizona and in adjacent southwestern Utah and southeastern Nevada, there exists a series of morphological subunits of the *lentiginosus* complex, most of which have been relatively unknown until rather recent times. Included are taxa that can be segregated, for the most part, into two groups by shape and inflation of the pods. One group, including vars. *oropedii* Barneby and *ambiguus* Barneby, has distinctly ovoid and inflated pods. Extralimital vars. *diphysus* (A. Gray) M. E. Jones, *vitreus* Barneby, and *wahweapensis* S. L. Welsh, likewise have ovoid, inflated pods. None of those are treated here. Rather this discussion centers on those entities with cylindrical or subcylindrical pods that are not greatly inflated, specifically, on var. *mokiacensis*, var. *palans*, and on var. *trumbulensis*, newly proposed herein.

Members of the group with cylindrical or subcylindrical pods have long been known, and have been summarized twice in the past several decades (Barneby 1945, 1964). Barneby’s discussions and subsequent realignment of the included taxa are presented under the varieties treated below.

1. Pods substipitate to short-stipitate, the stipe 0.1–1 mm long;

- leaflets pubescent on both sides (though sometimes sparsely so above); plants of the vicinity of Mt. Trumbull, Mohave Co., Arizona 2c. var. *trumbullensis*
1. Pods sessile; leaflets typically glabrous at least above; plants of various areas (2)
2. Pods spreading to descending, mainly hamately or rather uniformly incurved, deciduous; wing petals typically purple apically; plants of sw. Colorado and n. Arizona along and n. of the Colorado River to se. and sw. Utah 2a. var. *palans*
2. Pods erect-ascending, straight, steeply incurved-ascending, or rarely erect-ascending and decurved, persistent; wing petals typically pale or white apically; plants of the Beaver Dam Mts., and w. of Zion Canyon, Washington Co., Utah and adjacent Virgin Mts., nw. Mohave Co. Arizona and adjacent Clark Co., Nevada 2b. var. *mokiacensis*

2a. var. *palans* (M. E. Jones) M. E. Jones, Contr. W. Bot. 8: 4. 1898. [*Astragalus palans* M. E. Jones, Zoë 4: 37. 1893. TYPE: "Montezuma Cañon, Utah, Jun 1, 1892, coll. by Miss Alice Eastwood" (HOLOTYPE: POM; ISOTYPES: CAS, GH, MO, NY, UC).]

Perennial (sometimes short-lived); leaves (3.5–) 5–11 cm long; leaflets 13–21 (–23), (3–) 5–17 (–23) mm long, broadly obovate-cuneate, oblong-elliptic, oblong-ob lanceolate, or suborbicular-obcordate, obtuse, emarginate or subacute, flat or loosely folded; peduncles erect or incurved, shorter than or equalling the leaf; racemes loosely (6–) 10– to 28-flowered, the axis (1–) 2–12 (–14.5) cm long in fruit; calyx 6.3–9.4 mm long, either black- or white-strigulose, the tube 4.7–6.8 mm long, the teeth (0.9–) 1.1–3 (–4) mm long; flowers 13.5–17.5 (–18.3) mm long, pink-purple; pods spreading, declined, or spreading-ascending, obliquely linear-lanceolate to narrowly ovate-acuminate in outline, almost straight to uniformly or hamately incurved, (12–) 15–27 mm long, 4–8.5 mm thick, the unilocular beak 5–8 mm long, somewhat fleshy, green, glabrous or strigulose, becoming leathery or stiffly papery, stramineous (finally blackish), bilocular or nearly so; ovules 20–42.

HABITAT AND DISTRIBUTION. *Astragalus lentiginosus* var. *palans* flowers from April to June, and is found in salt desert shrub,

blackbrush, juniper, pinyon-juniper, and mixed desert shrub communities at 1130 to 1900 m in southeastern and southwestern Utah, southwestern Colorado, and northern Arizona. How far var. *palans* extends along the Grand Canyon is subject to continued investigations, but all known records are from some distance to the east of the Mount Trumbull area.

Barneby (1964: 956) notes that, “var. *palans* consists of numerous races differing further in density and distribution of the pubescence, size of flowers, and length of fruiting raceme.” He then cites specimens collected by Lemmon (3116, 3326), those with straight erect or ascending pods and leaves pubescent on both sides, as examples that might lead to further elaboration upon closer examination. He had treated them in his 1945 revision as part of var. *mokiensis*. Those specimens have not been examined by us, but it seems more than likely that they represent what is considered below as var. *trumbullensis*.

2b. var. *mokiensis* (A. Gray) M. E. Jones, Rev. N.-Amer. *Astragalus* 126. 1923. Mokiak milkvetch. [*Astragalus mokiensis* A. Gray, Proc. Amer. Acad. Arts 13: 367. 1878. *Tium mokiense* (A. Gray) Rydb. TYPE: “Mokiak Pass, on the borders of Utah and N. W. Arizona, Dr. Palmer, 1877” (HOLOTYPE: GH; ISOTYPES: K, NY 2 sheets, POM fragm., US. *A. ursinus* A. Gray, Proc. Amer. Acad. Arts 13: 367. 1878. *A. lentiginosus* var. *ursinus* (A. Gray) Barneby, Leaflet. W. Bot. 4: 133. 1945.]

Perennial, mostly 20–60 cm tall; leaves 3–10 (–13) cm long; leaflets (7–) 9–17 (–21), 5–13 (–19) mm long, broadly obovate-obcordate, lanceolate, elliptic, or suborbicular-obcordate, emarginate or retuse to truncate, flat, pubescent to glabrous above; peduncles erect or incurved, 4–11 (–14) cm long, shorter than the leaf; racemes loosely 12- to 20-flowered, the flowers ascending, the axis 3.5–15 (–20) cm long in fruit; calyx 5–8 (–9.2) mm long, either black-strigulose or mixed black- and white-strigulose, the tube (3.5–) 4–6.5 mm long, short-cylindric to campanulate, the teeth (0.9–) 1–2 (–2.7) mm long, subulate; flowers (10–) 14–18 (–19) mm long, pink-purple or pink- to red-purple with pale or white wing-tips, the banner recurved through ca. 50°; pods ascending-erect to ascending or rarely spreading, sessile, oblong-ellipsoid, almost straight to incurved or decurved, 14–28 (–32) mm long, 4.5–6.5 (–8) mm thick, the unilocular beak 3–4 mm

long, somewhat fleshy, green, glabrous or minutely pubescent, becoming leathery or stiffly papery, stramineous, bilocular or nearly so; ovules (22–24) 25–36; $n = 11$ (as var. *palans*).

HABITAT AND DISTRIBUTION. *Astragalus lentiginosus* var. *mokiacensis* flowers from March to June. It grows on limestone or outcrops and gravel or granitic gravels with *Hymenoclea*, bursage, Joshua tree, *Larrea*, and *Ferocactus* at 910 to 1750 m, in the Beaver Dam Mountains, Washington County, Utah, northwestern Mohave County (Grand Wash and vicinity), Arizona, and eastern Clark County, Nevada.

Placement of *Astragalus ursinus* within var. *mokiacensis* is justified on several bases. First, the reputed type locality in Utah has been ruled out by diligent search. Second, the collection by Palmer was labeled by C. C. Parry, subsequent to the arrival of specimens sent to him by Palmer at Davenport, Iowa, and it is almost certainly mislabeled. Probably it was collected by Palmer in northern Arizona at the same time as he collected the type of *A. mokiacensis*. The type, and only extant material of *A. ursinus*, closely resembles a slightly smaller flowered phase of var. *mokiacensis*, although plants with calyces matching the small size of those of the type of *A. ursinus* are still unknown within var. *mokiacensis*. Certainly, M. E. Jones, premier pioneer student of the complex in the American West, recognized the similarity by placing them within the same taxon as *A. ursinus*. He likewise discounted the presence of the taxon in Utah when he noted (Contr. W. Bot. 15: 21. 1929) that “*A. ursinus* . . . actually grows only in Arizona bordering the Grand Canyon.”

The summary treatment of the *lentiginosus* complex by Barneby (1945) included *Astragalus mokiacensis* at varietal rank. He had seen only three collections at that time that exactly matched the type, but concluded that, “The variety in its strict sense is very closely related to var. *palans*, var. *Wilsonii*, and var. *ursinus*, and all four should perhaps be united.” The var. *wilsonii* (Greene) Barneby is known from south of the Grand Canyon, and is excluded from treatment herein. Later, Barneby (1964: 580) removed *A. mokiacensis* from consideration within the *lentiginosus* complex, placing it instead within sect. *Preussiani*. He justified that decision on the basis of similarity of flowering specimens and juxtaposition of *A. preussii* A. Gray with the distribution of

Astragalus mokiacensis. However, all members of sect. *Preussiani* are evidently obligate selenophytes, with strictly unilocular pods. *A. mokiacensis* is, instead, an obligate or essentially obligate calciphile, occurring always or almost so on limestone substrates, typically on cliffs and rock outcrops; and it has bilocular or nearly bilocular pods.

With the rather large number of specimens of var. *mokiacensis* now available for study, we can find no consistent floral differences, aside from the pale or white wing tips, between this taxon and var. *palans*, with which it has been consistently confused in Washington Co., Utah. Even pod features do not differ in any consistent manner. However, the pods of var. *palans* tend to spread, and have erect-ascending tips, while those of var. *mokiacensis* are typically stiffly erect-ascending.

2c. var. **trumbullensis** S. L. Welsh & N. D. Atwood, var. nov.
TYPE: U.S.A. Arizona: Mohave Co., Mohave Strip, Andrus Canyon, 3 mi. W of Andrus Pt., T32N R10W S6, wash bottom with *Mortonia*, *Purshia*, *Ephedra*, *Agave*, etc., 26 Apr 1999, N. D. Atwood & B. Furniss 24293 (HOLOTYPE: BRY; six isotypes to be distributed).

Plantis similis vars. *mokiacensi* et *palanti* sed in leguminibus subsessilibus vel stipitatis e uterque in foliolis pubescentibus utrinque differt.

Perennial, mainly 30–35 cm tall; leaves 2–9.5 (–10.5) cm long; leaflets (7–) 13–17, 5–15 mm long, 2.5–8 mm broad, broadly obovate to oblanceolate or elliptic, retuse to rounded or subacute, flat, strigulose on both sides; peduncles erect or erect-ascending, 4.5–7.5 cm long, shorter than to somewhat surpassing the leaf; racemes loosely 4–15 (–17) -flowered, the flowers ascending, the axis 3–6.5 (–7.5) cm long in fruit; calyx 6.3–7.4 mm long, the tube 4.8–5.5 mm long, deeply campanulate, the teeth 1.7–2 mm long, triangular-subulate; flowers 13–17 mm long, pink-purple or pink- to red-purple with pale or white wing-tips, the banner recurved through ca. 40°; pods ascending-erect to ascending, subsessile to short stipitate, the stipe (gynophore) 0.1–1 mm long, the body linear-oblong to oblong or narrowly elliptic in profile, 17–32 mm long, 4–5.5 (–8.5) mm thick, subterete, the unilocular beak 3–5 mm long, somewhat fleshy, stramineous or mottled,

strigulose, becoming leathery or stiffly papery, bilocular or nearly so; ovules 14–32.

ADDITIONAL SPECIMENS (PARATYPES; all BRY!): ARIZONA: Mohave Co., Parashant (Trail) Canyon, 11 mi. S of Mt. Trumbull Village, 26 Apr 1974, *Atwood 6029, 6029a*; ditto, Whitmore Canyon, 1.25 km (7.8 mi.) S of Mount Trumbull (abandoned town), T34N R9W S29, 25 May 1979, *Holmgren & Barneby 9172*; Daneill Canyon W of Andrus Canyon, 3 mi. W of Andrus Pt., T32N R11W S12, 26 Apr 1999, *Atwood & Furniss 24300*; ditto, Andrus Canyon, 1 mi. W of Andrus Pt., T32N R10W S10, 26 Apr 1999, *Atwood & Furniss 24302*; ditto, Whitmore Canyon, T32N R9W S1, 27 May 1999, *Higgins 20226*; ditto, 2 mi. S of Mt. Trumbull school house, near Griffith Knoll, T34S R10W S1–2, 27 May 1999, *Higgins 20277*.

HABITAT AND DISTRIBUTION. *Astragalus lentiginosus* var. *trumbullensis* flowers in April. This variety is found on sandstone outcrops and gravel, with *Mortonia*, *Purshia*, *Ephedra*, *Agave*, and other warm-desert shrubs at 910 to 1750 m, in canyons subsequent to the Colorado River, Grand Canyon, Arizona (Figure 3).

The material on which the above description is based has racemes loose as in both vars. *palans* and *mokiensis*, but the raceme axis is shorter than that of the latter entity, i.e., 3–6.5 (–7.5) cm versus 5–15 (–20) in *mokiensis*, and both of the varieties have sessile pods. However, leaflets of var. *trumbullensis* are pubescent on both sides (though sometimes thinly so above), unlike those of both vars. *palans* and *mokiensis*, which are typically glabrous on one or both sides. Specimens have long been known, and the early collections cited above misled these workers into initial placement of them with var. *mokiensis*.

MALVACEAE

Sphaeralcea grossulariifolia (Hook. & Arn.) Rydb.

var. **fumariensis** S. L. Welsh & N. D. Atwood, var. nov. TYPE: U.S.A. Utah: Kane Co., west side, Little Valley, N of Lake Powell, T41S R6E S19, 6 May 1998, *S. L. Welsh & N. D. Atwood 26968* (HOLOTYPE: BRY!; five isotypes distributed previously as *Sphaeralcea grossulariifolia*).

Similis var. *grossulariifolia* in aspectem et amplitudinem sed pilis grose hirsuti-stellatis et carpelis obscure fenestratis differt.

ADDITIONAL SPECIMENS (PARATYPES; all BRY!): UTAH: Kane Co., head of



Figure 3. *Astragalus lentiginos* Douglas ex Hooker var. *trumbullensis* S. L. Welsh & N. D. Atwood (composite of Atwood & Furniss 23293 and 24300 BRY).

Smoky Hollow dugway, T41S R4E S8, 17 Jun 1998, *Atwood & Welsh* 23859; Tibbett Spring, T41S R3E S32, 20 May 1999, *Atwood et al.* 24598; ca. 7 mi. W of Smoky Mt., head of Creeks Rd., T40S R3E S36, 20 May 1999, *Atwood et al.* 24614; ca. 7 mi. W of Kelly Grade, Croton Junction, T43S R3E S14, 20 May 1999, *Atwood et al.* 24627; Drip Tank Canyon, E of Four Mile Bench, T40S R3E S24, 6 May 1998, *Welsh & Atwood* 26938; Reeses Canyon, ca. 2 mi. N of confluence of Last Chance Canyon/Reeses Canyon, T40S R4E S36, 21 May 1999, *Atwood et al.* 24638.

HABITAT AND DISTRIBUTION. *Sphaeralcea grossulariifolia* var. *fumariensis* is found with shadscale and creosote bush, and in other mixed desert shrub communities at 1220 to 1985 m in the vicinity of Smoky Mountain, eastern Kane County, Utah. It is endemic (Figure 4).

This phase of the widely distributed *Sphaeralcea grossulariifolia* has been known since it was first observed in the 1970s, during baseline studies of the then proposed Navajo and Kaiparowits electrical generating stations. No specimens were collected at that time, but the memory of them persisted through the decades until another opportunity at understanding the flora was triggered by the establishment of the Grand Staircase-Escalante National Monument.

In general aspect, var. *fumariensis* (name derived from Smoky Mountain and the Burning Hills portions of the Kaiparowits Plateau) closely simulates plants of var. *grossulariifolia*, whose distribution is contiguous, but evidently not within its range. Plants of var. *fumariensis* are geographically correlated with the Straight Cliffs Formation, and especially with that portion modified by natural fires that burned the coal in situ, resulting in thermally modified, red, brown, or yellow strata that tumble downward into the canyons as variegated, steep talus slopes.

The plants are at once notable because of their gray-hoary appearance, which results from the harsh, coarse, hirsute-stellate pubescence. That appearance differs markedly from both the green, thin-leaved var. *moorei* S. L. Welsh, which occurs along Glen Canyon to the east, and from var. *grossulariifolia* which is widespread elsewhere in Utah and the West.

Additionally, the carpel faces are only obscurely, if at all, fenestrate. The character of fenestrate faces is variable within the species as a whole, but the fenestrae are generally present elsewhere in the species.



Figure 4. *Sphaeralcea grossulariifolia* (Hooker & Arnot) Rydberg var. *fumariensis* S. L. Welsh & N. D. Atwood (Atwood & Welsh 23859 BRY).

The following key will serve to segregate the varieties of the species.

1. Herbage bright green; leaves thin-textured, often narrowly lobed; plants of the vicinity of Glen Canyon, eastern Kane and Garfield, and w. San Juan, Cos., Utah . . var. *moorei*
1. Herbage gray green or ashy green to whitish canescent or hirsute-stellate; leaves thick-textured, variously but often broadly lobed; plants with distribution as noted below . . .
..... 2
2. Pubescence appressed or subappressed and finely stellate, the longest trichome hairs 0.15–0.3 (–0.4) mm long; plants widespread in the American West
..... var. *grossulariifolia*
2. Pubescence coarsely hirsute-stellate, the longest trichome rays up to 0.5–0.7 (–1.1) mm long; plants of Smoky Mt. and Burning Hills vicinity, e. Kane Co., Utah . . .
..... var. *fumariensis*

ONAGRACEAE

Oenothera murdockii S. L. Welsh & N. D. Atwood, *sp. nov.*
Chinle evening-primrose. TYPE: U.S.A. Utah: Kane Co., clay-silt of Chinle Formation, *Phacelia-Eriogonum-Astragalus* community, at 1700 m, Kitchen Corral Canyon, ca. 1 mi. W of Kitchen Corral Point and 6 mi. SW of Mollies Nipple, T41S R3W S33, red-purple outcrops, sparsely vegetated in pinyon-juniper community, 5 Jun 1993, S. L. Welsh 25643 (HOLOTYPE: BRY!; 3 isotypes distributed previously as *O. flava*).

Ab *Oenothera flava* (A. Nelson) Garrett in duratione annuis vel heime annuis radic-surculis axe petalis brevioribus (9–12 nec plerumque 15+ mm) absimilis, et a *O. primiveris* A. Gray in foliis puberulentis nec longipilis sepalis et petalis majoribus et capsulis non-alatis differt.

Annual acaulescent herb, with a heavily lignified taproot and simple shoot-crown, this long-persistent following death; leaves basal, 4–17.5 cm long, 0.5–3.5 cm wide, subentire or more commonly toothed or pinnatifid, the terminal lobe 1.5–5.5 cm long, 0.7–2.1 cm wide, puberulent to subglabrous; flowers clustered, solitary in leaf axils; hypanthium 2.5–4.5+ cm long; sepals 0.8–1.3 cm long, reflexed as a unit or two by two and with red mar-

gins or red overall; petals 9–12 mm long, yellow, drying yellow or orange-brown; capsules 1.3–2.5 cm long, evidently winged above the middle, the wings 3–7 mm wide; seeds in 2 rows per locule, 2.2–2.7 mm long.

ADDITIONAL SPECIMENS (PARATYPES; all BRY!): UTAH: Kane Co., Paria River, Paria, 1 May 1957, *Murdock 117*; ditto, 17 mi. E of Kanab, T43S R41/2W S34, 9 May 1987, *Franklin 4650A*; ditto, as for the holotype, 18 May 1994, *Welsh 25306*; ditto, 5 May 1998, *Welsh & Atwood 26921*; ditto, 17 May 1999, *Atwood, Welsh & Spencer 24473, 24478*; east of mouth of Fin Little Canyon, T42S R3W S8, *Atwood & Welsh 23901*; Washington Co., T42S R11W S14, 4 mi. SE of Rockville on rd. to Smithsonian Butte at junction of Wire Mesa Rd., 17 Jun 1987, *Thorne, Clark & Welsh 5385*.

HABITAT AND DISTRIBUTION. *Oenothera murdockii* occurs on Chinle and Moenkopi (?) formations barrens, with *Phacelia demissa*, *Eriogonum subreniforme*, and *Astragalus ampullarius* in the pinon-juniper community at 1350 to 1750 m in Kane and Washington Counties, Utah. The species is endemic (Figure 5).

The Chinle evening-primrose has long been mistaken for the similar *Oenothera flava*, with which it is compared in the diagnosis. That plant occurs mainly at middle to upper elevations, often in mesic habitats. It is clearly perennial, the root-shoot axis not or hardly lignified, and the flowers are larger in all parts, even if the smaller ones overlap with those of the present proposal.

The plant, a survivor of harsh edaphic conditions, is named in memory of the late Joseph Richard (Dick) Murdock, who collected the earliest specimens of the species at BRY, and whose ecological specialty involved soil-plant relationships.

RANUNCULACEAE

The genus *Aquilegia* consists of a series of taxa that differ in rather inconsequential manners, especially as regards their basic structure (Munz 1946). That is, the leaves are practically always biternate or triternate, with taxa in which the former is generally the case having, on occasion, triternate leaves. The same is true for other vegetative features, and often for the floral ones as well. Proportion of flowers, including length-width comparisons, exsertion of stamens beyond the petal blades, length of petal spur to total flower length-width ratios, and length of sepals to spur length ratios seem to be of fundamental importance, however.

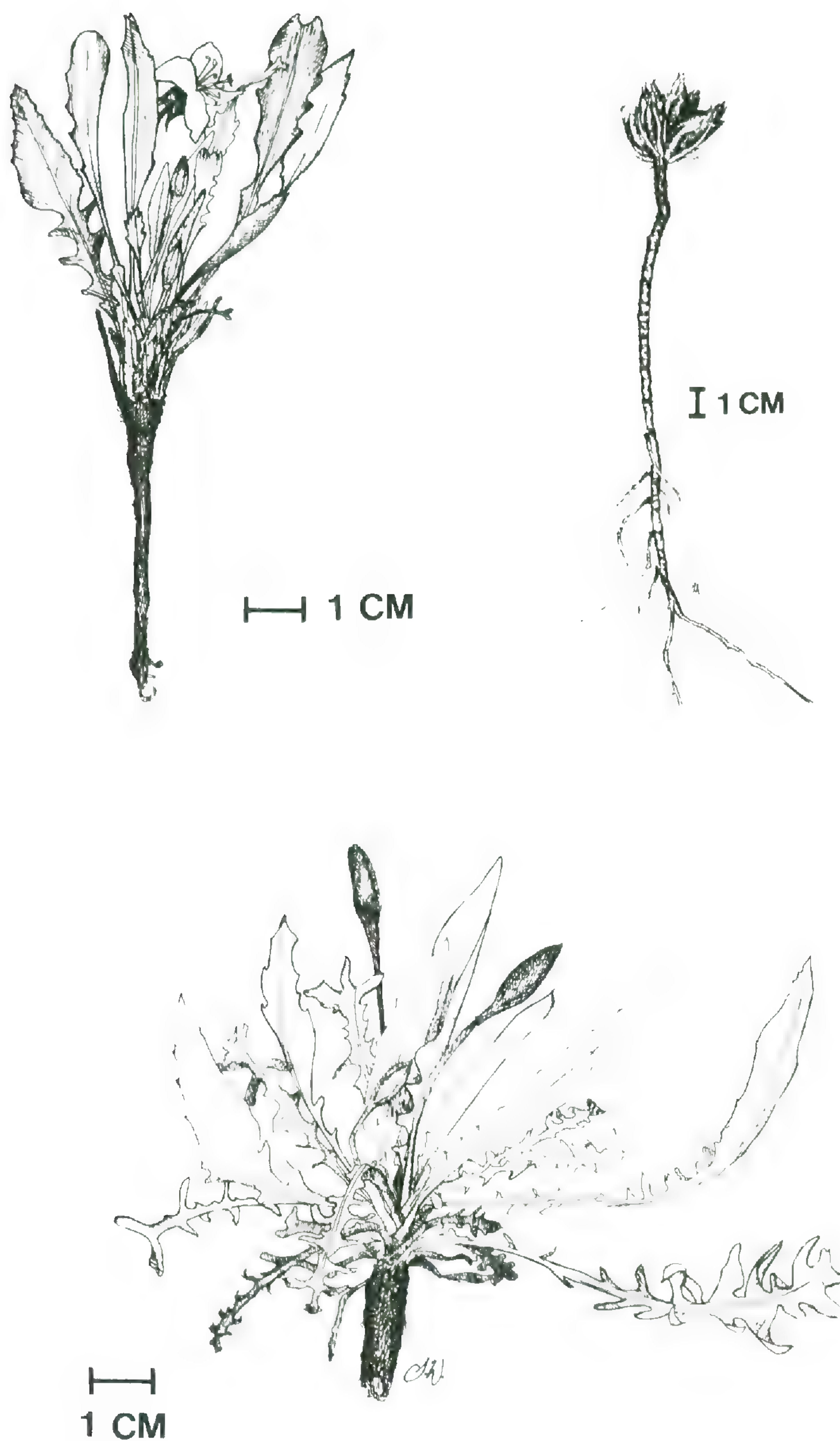


Figure 5. *Oenothera murdockii* S. L. Welsh & N. D. Atwood. Top left: Flowering plant (Atwood, Welsh & Spencer 24479 BRY). Top right: Dead plant with capsules from previous year (Welsh & Atwood 26921). Bottom: Plant in bud (Welsh & Atwood 26921 BRY).

Flower color is helpful to an extent, but in some taxa there is so much variation in flower hue as to negate its usefulness as a diagnostic tool. Payson (1918) discussed the problem of lack of diagnostic criteria in the genus. The species, despite the failure of any single morphological criterion as diagnostic, are rather readily identifiable in the field, and most often in the herbarium. Minute differences in measurements of any of the parts might not aid in identification, or in definition of the taxa, but the taxa tend to be isolated either geographically or ecologically from one another, and are therefore readily identifiable.

The two novelties described below do not fit well within any of the species of columbine known for Utah, and are therefore presented as new.

Aquilegia desolaticola S. L. Welsh & N. D. Atwood, *sp. nov.*
 TYPE: U.S.A. Utah: Grand Co., Desolation Canyon, Green River, Rattlesnake tributary, T18S R17E S32, 10 May 1999, *N. D. Atwood & A. Evenden 24464* (HOLOTYPE: BRY!; isotypes (4) to be distributed).

Similis *Aquilegia chrysantha* A. Gray in floribus coloratis sed in magnitudine et folis biternatis et foliis segmentis incrassatis differt, et ab *A. barnebyi* Munz in floribus aureus nec aurantiacis vel miniatis et in foliis amplitudine et segmentis incrassatis ab-similis.

Plants mainly 4–6 dm tall; stems glabrous throughout or puberulent only above, forming large clumps, the caudex bases with conspicuous thatch of marcescent leaf bases; basal leaves (7–) 15–35 cm long, biternate, glabrous on both sides, the ultimate segments 1.8–5 cm long, 3.2–5.8 cm wide, the petioles 10–30 cm long, the petiolules 4–7 cm long; cauline leaves mainly 2 or 3 developed, the uppermost bracteate; pedicels mostly 3–7 cm long; flowers 1 to several, nodding, longer than broad; sepals horizontally spreading, 13–16 (–18) mm long, clear golden yellow or slightly suffused with or fading bluish or pinkish or fading yellowish throughout, elliptic to lance-elliptic; petals with spurs yellow, the blades golden yellow, 7–10 mm long; spurs 2.5–3.5 cm long; stamens exceeding blades by 7–12 mm; follicles 5–7, 1.7–2.5 cm long, puberulent.

ADDITIONAL SPECIMENS (PARATYPES): UTAH: Grand Co., T19S R16E S1, ca.

13 mi. due NNE of Green River, re-entry off Gray Canyon, at 4320 ft. elev., 28 May 1988, *Franklin 6124*; ditto, Desolation Canyon, Green River, below Coal Creek, Gray Canyon, T18S R17E S29, 10 May 1999, *Atwood & Evenden 24462*; Uintah Co., Desolation Canyon, Green River, across from Nutters Rock, T13S R17E S26, 10 Sep 1999, *Johnson 99-127, 99-141*.

HABITAT AND DISTRIBUTION. *Aquilegia desolaticola* inhabits seeps and adjacent moist sandy soil in the Tertiary Price River Formation along the Green River in canyons tributary to Desolation Canyon, at elevations of 1300 to 1350 m. to Grand and Uintah Counties, Utah. The species is endemic (Figure 6).

The flower color is much like that of *Aquilegia chrysantha*, but the taxon is probably most nearly allied to *A. barnebyi*, from which it differs in flower color, the longer and larger, biternate leaves, longer sepals, thicker leaf segments, and general habit. The caudex is conspicuously clothed with thickened marcescent leaf bases, which persist for many years in clumps. In this feature, the plants are unlike those of any other species in the state of Utah, with the exception of occasional specimens of long-persistent *A. micrantha*.

Aquilegia fosteri (S. L. Welsh) S. L. Welsh, *comb. nov.*, based on *A. formosa* var. *fosteri* S. L. Welsh, Great Basin Naturalist 46: 259. 1986.

Plants of this distinctive taxon have red and yellow or pink and yellow flowers and an overall glandular condition. Its more typical habitat is in perched crevice sites high along the Navajo and Kayenta sandstone walls of Zion Canyon. The seeds cascade downward from these high perches into the canyon proper where they germinate in moist sites, often clinging to vertical walls. Here the survivors hybridize with the golden-flowered, canyon bottom *Aquilegia chrysantha*. The resulting hybrids lack the distinctive glandular foliage, and have somewhat larger flowers intermediate in size between *A. fosteri* and *A. chrysantha*, often with very broad and pale spurs. The flowers of the hybrids and back-crosses do not retain the glandular condition and have flowers simulating the color, but not the proportions, of *A. formosa*, within which this taxon was previously named.

This entity has been annotated recently by A. T. Whitmore as belonging, in some part, to the look-alike, *Aquilegia desertorum* (M. E. Jones) Cockerell, a taxon that is not glandular-pubescent



Figure 6. *Aquilegia desolaticola* S. L. Welsh & N. D. Atwood (Atwood & Evenden 24464 BRY).

overall and which occurs at moderate elevations in northern Navajo and Coconino Counties, Arizona. Evidently that entity, in addition to lacking glandular pubescence in its lower parts, has shorter sepals (8–10 mm) and shorter spurs (15–22 mm). The occasional glabrous specimen from Zion Canyon appears to represent a back-cross between *A. fosteri* and *A. chrysantha*, or possibly it is nothing more than a part of the normal range of variation of the taxon.

Aquilegia loriae S. L. Welsh & N. D. Atwood, *sp. nov.* TYPE: U.S.A. Utah: Kane Co., Deer Spring Canyon, T41S R3W S7, ca. 5 mi. due W of Mollies Nipple, 37°15'0.3"N, 112°09'522.6"W, seep line ca. 450 ft. long, ca. 8 ft. high, with *Carex aurea*, Moenave Sandstone, hanging garden, at ca. 5840 ft., 14 Aug 1995, S. L. Welsh, N. D. Atwood & L. Armstrong 26178 (HOLOTYPE: BRY!; several isotypes to be distributed).

Similis *Aquilegia fosteri* (S. L. Welsh) S. L. Welsh in habitu et foliis glandular-pubescentibus sed in sepalis et calcaribus longioribus absimilis, et *A. micrantha* Eastw. similis sed in floribus coloratis roseis vel salmoneis nec albidis et staminibus laminis minus longioribus differt, et ab *A. desertorum* (M. E. Jones) Cockerell in foliis glandular-pubescentibus nec glabris et petalis laminorum longioribus differt.

Perennial herbs, mainly 2.8–6.5 (–7.5) dm tall, 1–3.2 mm thick, simple to several-branched, glandular pubescent below and above or only above; basal leaves 0.8–3.5 dm long, biternate to triternate, with rather thin, green segments, and glandular-puberulent on both surfaces, or thickened and glabrous; petioles 8–22.5 mm long; primary petiolules 1–4.7 cm long, the secondary ones 0–1.5 (–2) cm long; leaflets cuneate-obovate to orbicular or broader, 0.5–3.5 cm long, cleft ca. 1/3 to 1/2 their length, the divisions again cleft or with rounded lobes; cauline leaves usually present, the lower ones sometimes well-developed, the uppermost bracteate; flowers 1 to several, nodding; sepals ascending to spreading, red-maroon to pink, elliptic to lance-oblong, 8–13 mm long, 4–6 mm wide, acute; petal blades cream-colored, 5–8 mm long, broadly rounded, the spurs red-maroon to pink, 15–22 mm long, 2.5–4 mm wide at base, gradually tapering, the glandular tip bent but not recurved; stamens exceeding the petal blades by 7–12 mm, the anthers 1.2–2 mm long, the staminodia somewhat shorter

than the stamens, linear-lanceolate, sometimes bearing abortive (?) anthers; follicles glandular puberulent, 15–20 mm long, the tips spreading, the styles 4–10 mm long.

ADDITIONAL SPECIMENS (PARATYPES; all BRY!): UTAH: Kane Co., ca. 1/4 mi. S of cabins, near head of Wahweap Creek, Four Mile Bench, 16 Jun 1974, *Welsh & Wood 12440a*; near head of Wahweap, T39S R1E S33, 6 Jul 1994, *Welsh & Moore 25323*; ditto, 16 Aug 1995, *Welsh, Atwood & Armstrong 26187*; ditto, 20 Jun 1998, *Atwood & Welsh 23922a*; ditto, 22 May 1999, *Welsh, Atwood & Spencer 27387*; Lick Canyon, tributary of Riggs Canyon, W of No Man's Mesa, 15 Jun 1998, *Welsh & Atwood 27043*; ditto, 1 Oct 1998, *Welsh et al. 27169*; ditto, 18 May 1999, *Atwood, Welsh & Spencer 24480*.

HABITAT AND DISTRIBUTION. *Aquilegia loriae* grows in hanging gardens, moist canyon walls, and sand-seeps in the Straight Cliffs, Moenave, and Navajo Sandstone formations at elevations of 1780 to 1915 m. The species is endemic to Kane County, Utah (Figure 7).

On the Four Mile Bench in eastern Kane County, Utah, both *Aquilegia micrantha* and *A. loriae* grow juxtaposed, but not exactly within the same habitats. Where they grow adjacent to one another at Tommy Water and in the head of Wahweap Canyon, *A. micrantha* occupies drier simple driplines in the Straight Cliffs Formation sandstone, while *A. loriae* occurs in adjacent meadows and as a portion of the ground layer in small clumps of western birch. The distribution of *A. micrantha* is disjunct across that of *A. loriae*, extending west to as far as Water Canyon, west of Kanab, Utah. Intermediates have not been identified where the two taxa grow in close proximity. Most of the known habitat for *A. loriae* is within the newly established Grand Staircase–Escalante National Monument.

This taxon is named in honor of Lori Armstrong, a student of Utah botany who is dedicated to understanding the distribution of Utah's rare plants. It demonstrates considerable variation, as is the rule for practically all taxa within the genus. The main variation in *Aquilegia loriae* involves plant height, degree of viscid-ity, thickness of leaves, and overall flower size. Some plants from below the cabins in upper Wahweap Canyon show a trend from tall plants with glandular pubescence on lower stems, petioles, and petiolules but not on the leaflets, to much smaller plants that lack glandular pubescence on all lower plant parts. Both of those



Figure 7. *Aquilegia loriae* S. L. Welsh & N. D. Atwood (Welsh, Atwood & Armstrong 26178 BRY).

are here considered as a portion of the normal range of variation of the species. First flowers to open, as is the case with practically all members of *Aquilegia*, are frequently the largest, with those produced later in the season being smaller. The flowers within this taxon vary within rather narrow limits.

This entity differs in subtle ways from *Aquilegia desertorum*, but it does so in characteristics that are considered to be of importance in segregation of taxa. Not only is the lower part of the herbage glandular-puberulent in most materials of *A. loriae*, but the petal blades are evidently consistently shorter, 4–5 (not 7–12) mm. There are other minor differences in the flower parts and in their proportions to each other. Furthermore, the taxa are disjunct from each other by more than 200 km.

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LIFE CYCLE, DEMOGRAPHY, AND REPRODUCTIVE
BIOLOGY OF HERB ROBERT (*GERANIUM
ROBERTIANUM*)

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ABSTRACT. For nine years I studied the life cycle, demography, and reproductive biology of a woodland herb, *Geranium robertianum*, in central Massachusetts. These plants are facultative biennials that typically flower in the year after germination. Of 408 seeds experimentally sown in natural habitat, 26% gave rise to seedlings within six years. Of 1352 marked, naturally occurring seedlings, 53% survived to the end of their first growing season, 13% of plants alive at the end of their first growing season survived to year two, and 54% of these flowered. Plants germinating in early spring were more likely to survive to the end of year one and to flower than those germinating later in the year. Low summer rainfall appeared to reduce summer survival and low winter temperatures combined with little snow cover seemed to reduce winter survival. Floral structure and development, pollen-ovule ratios, and pollinator activity all suggest that plants of this species are highly self-pollinated. Herb Robert is one of only a few biennials that occupy undisturbed forest habitat.

Key Words: biennial, demography, facultative biennial, *Geranium robertianum*, herb Robert, life cycle, life history, self-pollination

Biennials are rare, comprising only 1.4% of the 14,500 species in the provisional checklist of the Flora of North America (Hart 1977). Plants with this life cycle pattern often are said to be associated with disturbed habitats (Kelly 1985; Silvertown 1984), although a few biennial herbs of relatively undisturbed habitats, such as forests, are known (Morgan 1971).

Numerous hypotheses have been proposed regarding the adaptive significance of bienniality (Bender and Baskin 1994; Hart 1977; Meidjen et al. 1992; Schaffer and Gadgil 1975; Silvertown 1984), but our current knowledge of biennial species is insufficient to decide which, if any, of these hypotheses is correct. Given this state of knowledge, examination of the natural history of additional biennial species is desirable.

Here I present an ecological investigation of a putative biennial, *Geranium robertianum* L. (herb Robert, Geraniaceae), emphasizing the species' life cycle and two areas potentially relevant

to interpreting the life cycle: demography and reproductive biology. My specific objectives were to 1) determine what life cycle pattern this species possesses; 2) understand the timing and causes of mortality; 3) investigate the relationship between germination time, vegetative growth, and flowering; and 4) describe the flowering phenology and breeding system.

Geranium robertianum is a forest herb that has been referred to as a biennial, but also as an annual, a winter annual, and a monocarpic or polycarpic perennial (Baker 1956; Falinska and Piroznikow 1983 and references therein; Fernald 1950; Gleason and Cronquist 1991; Widler-Kiefer and Yeo 1987; Yeo 1973). Even within North America, the species has been described as an annual (Fernald 1950), an annual or winter annual (Great Plains Flora Association 1986), and an annual or biennial (Gleason and Cronquist 1991).

Herb Robert occurs in northeastern North America, Eurasia, and northern Africa (Baker 1957; Widler-Kiefer and Yeo 1987). The North American range extends from Newfoundland to Maryland, west to Illinois (Fernald 1950). The species has been introduced to western North America, New Zealand, and Singapore (Baker 1957).

Herb Robert typically occurs in shady or partly shaded habitats, and often is associated with rocky ground and nutrient-rich or basic soils (Baker 1956; Falinska and Piroznikow 1983; Voss 1985). In North America, the habitat of herb Robert is described as “damp rich woods” (Gleason and Cronquist 1991), “rocky woods, ravines and gravelly shores” (Fernald 1950), and “rich deciduous woods . . . clearings, along roads and trails . . . rocky openings, gravelly shores and rubble” (Voss 1985). In New England the species is listed as “occasional” by Seymour (1969). It is absent from several Massachusetts coastal counties and is rare in Rhode Island (George 1996; Sorrie and Somers 1999). In central Massachusetts, the species occurs sporadically and is restricted largely to rocky wooded slopes with soils that are seemingly richer and/or less acid than the norm.

MATERIALS AND METHODS

Field work. I conducted field work at two sites in Princeton, Massachusetts (42°28'N, 71°54'W). Herb Robert plants at both sites grew among boulders in rocky woodland. Because much of

the ground surface was occupied by boulders, plots were placed arbitrarily rather than randomly to avoid including large areas of unvegetated rock.

One study site was at an elevation of 350 m on a south-facing slope in Wachusett Meadow Wildlife Sanctuary of the Massachusetts Audubon Society. Dominant trees at this site were shagbark hickory [*Carya ovata* (Miller) K. Koch], white ash (*Fraxinus americana* L.), and sugar maple (*Acer saccharum* Marshall), with hornbeam [*Ostrya virginiana* (Miller) K. Koch] common in the understory. Two plots were arbitrarily selected on this slope in the spring of 1990. Plot A occupied 0.72 m² with little vegetation other than herb Robert present. Plot B was 12 m from plot A, comprised 1.82 m², and contained a fern [*Dryopteris marginalis* (L.) A. Gray], Virginia creeper [*Parthenocissus quinquefolia* (L.) Planchon] and the goldenrod *Solidago caesia* L.

The second site was 2.7 km from the first site, in Wachusett Mountain State Reservation, at an elevation of 430 m. The dominant woody plants on this ESE-facing slope were white ash, sugar maple, shagbark hickory, hornbeam, red elderberry (*Sambucus racemosa* L.), and alternate-leaved dogwood (*Cornus alternifolia* L.f.). Plot C, established in 1990, was 0.82 m² and contained Jack-in-the-pulpit [*Arisaema triphyllum* (L.) Schott.], enchanter's nightshade (*Circaea lutetiana* L.), and fringed bindweed (*Polygonum cilinode* Michx.). A second plot (D) was established at this site in 1995 to increase the number of plants being monitored. It included little vegetation besides herb Robert.

Plots were visited starting in late April or early May in each year between 1990 (1995 for plot D) and 1998. The plots were visited weekly until late June and at two- to three-week intervals thereafter until late September or early October. I also visited the plots four times in 1999 to determine the fate of the 1998 cohort. Newly germinated plants were recognized by their cotyledons and small size. Each was monitored throughout its life following marking with a numbered plastic stake secured to the plant with a plastic twist tie. During each visit I recorded the number of leaves on each plant as an indicator of plant size. For reproductive plants, I recorded the numbers of flowers and fruits and used the maximum recorded sum of flowers and fruits as a conservative estimate of total flower production for each plant. Substrate depth was measured for each plant at the time of its death by pressing a plastic knitting needle marked in 1 cm increments down into

the humus at the base of the plant until it reached a rock or a depth of 12 cm. The length of the concealed portion of the needle was taken as the substrate depth.

To examine the demography of dispersed seeds, I sowed seeds into twelve 60 cm diameter plots at Wachusett Meadow in 1993. Plots were chosen on the same rocky hillside as plots A and B, and the center of each was marked with a numbered plastic stake. Each seed demography plot was at least 2.0 m from the nearest herb Robert plant to minimize the possible presence of any naturally occurring herb Robert seeds, but was in habitat that appeared to be appropriate for the species. Seeds were collected from naturally growing plants at Wachusett Meadow and sown in the plots. Each plot received 10 seeds on July 14, 7 on July 16, 9 on July 19, 4 on July 25, and 4 on August 8, for a total of 34 seeds. The variation in these numbers reflects the natural variation in seed supply during the summer. Seeds were scattered on the surface of the leaf litter, as they would be during natural dispersal, within 30 cm of the center of the plot. The plots were monitored for seedlings at 1–3 week intervals during the remainder of the 1993 growing season and in each of the 1994–1998 growing seasons, and four times during 1999. The area between 30 cm and 150 cm from the plot center also was monitored during these visits to detect any additional seedlings that might suggest the presence of a naturally occurring seed bank in or near these plots.

I made field observations of floral development and pollinator activity using 38 marked flowers on a total of twelve plants near plots A and B in early June, 1993 at Wachusett Meadow. I collected one flower from each of five plants at each site to determine pollen/ovule ratios (see below).

Information on weather conditions was obtained from two locations. Temperature and precipitation records were obtained from the weather station at the Worcester airport. This station is 300 m above sea level and 22 km S of the study sites. I obtained daily records of winter snow cover from this station until October, 1995 when the weather station ceased recording this information. From October, 1995 through April, 1999 snow cover records were recorded at the author's residence in Paxton, Massachusetts, 15 km SSW of the study sites, at an elevation of 318 m.

Laboratory studies. Seeds from the Princeton, Massachu-

setts populations were unavailable when laboratory investigations were conducted; instead I used eight plants established from seeds collected in Hinesburg, Vermont. Plants were grown in 8 cm square pots containing Metromix 350, a soil-less growth medium. Plants were overwintered in a greenhouse at a temperature just above freezing, and were then moved to a growth chamber for further study. The temperature in the chamber was 25°C during each 14 hr. day and 15°C during each 10 hr. night.

The ability of flowers to self-pollinate was examined in a growth chamber in the absence of insects. I used four experimental treatments: 1) hand self-pollination, 2) hand cross-pollination, 3) no pollination, and 4) emasculation and no pollination. Treatments were assigned randomly within two or three blocks of four flowers on each of eight plants. The stigmas of hand-pollinated flowers received large loads of pollen from a toothpick on all five stigmas. Emasculation involved removing anthers with fine forceps shortly after the flowers opened. Any pollen inadvertently deposited on stigmas was removed by wiping with moist cotton under a dissecting microscope. Seeds were counted at fruit maturation.

One flower from each of four Vermont plants was collected and, in addition to the five flowers from each Massachusetts site, used to determine pollen/ovule ratios. The number of ovules in each flower was counted under a dissecting microscope. One anther from each flower was emptied into a small Petri dish containing 70% alcohol and the pollen grains, which are large in this species, were counted over a 2 mm $\times$ 2 mm grid using a dissecting microscope.

Data analysis. Sample sizes from individual field plots were too small for most analyses, so I lumped data for all four plots. This lumping violates the assumption of independence of observations, and this shortcoming should be considered in interpreting results. However, general trends were usually similar in the four plots. For example, correlations between plots A, B, and C in numbers of seedlings over nine years were all significantly positive ($r > 0.67$, $P < 0.05$). No correlations between plot D and the other plots were significant, though these tests were not very powerful because I had only four years of data for this plot.

I used three kinds of analyses for field data. I used G-tests to evaluate independence of variables for frequency data (e.g., num-

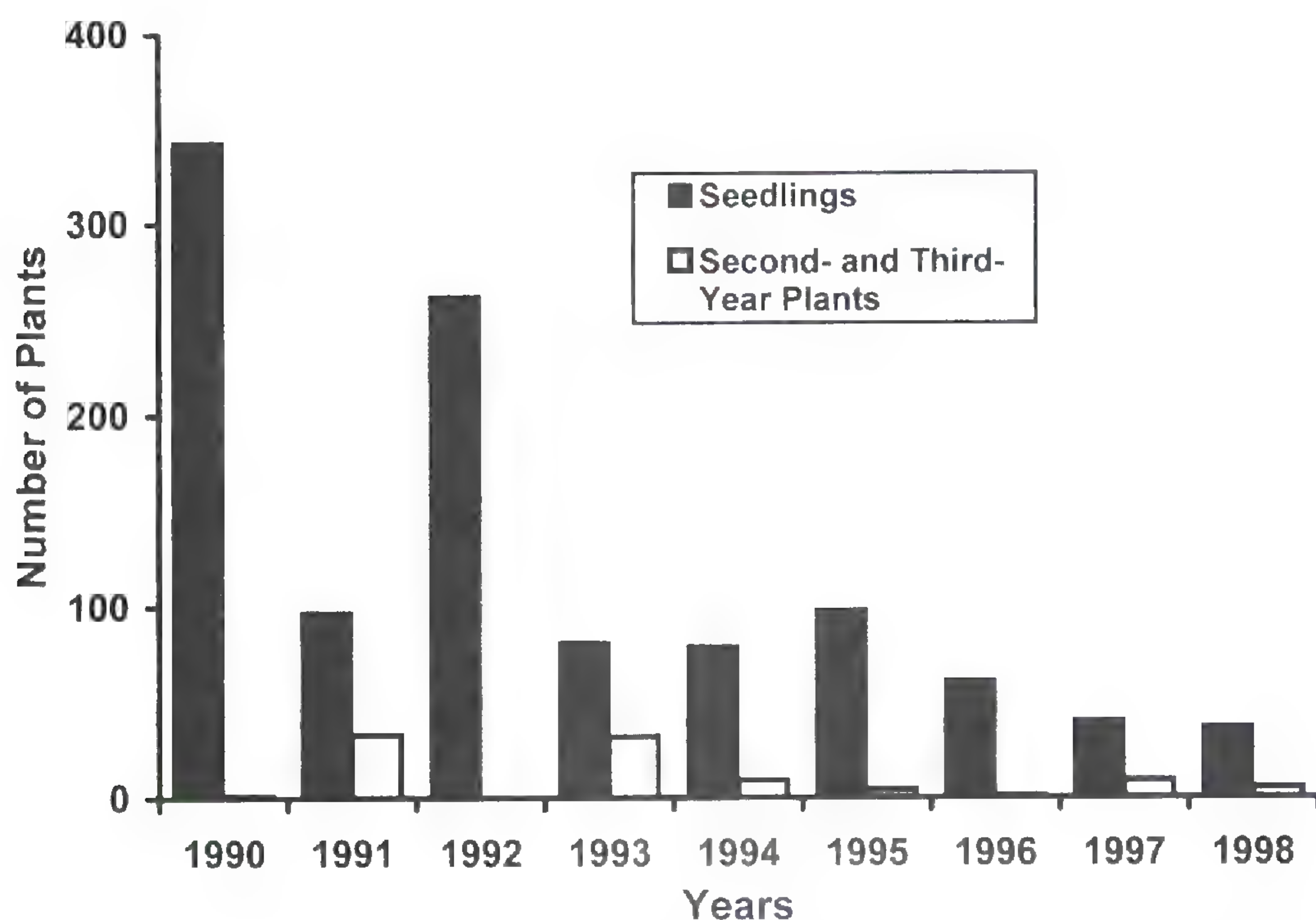


Figure 1. Numbers of seedlings and older (2nd- and 3rd-year) plants in plots A–C in nine years. Second and third year plants represent survivors from earlier years.

ber of survivors and non-survivors in different years). I used product-moment correlations to evaluate associations between continuous variables, such as proportion surviving and amount of precipitation in different years. Finally, I used a t-test to compare the numbers of flowers produced by early- and late-emerging seedlings.

RESULTS

Plant demography. A total of 1352 seedlings was marked between 1990 and 1998, and each seedling was monitored for its entire life. Considering just plots A–C, which were monitored for the entire study, the numbers of emerging seedlings varied from 37 in 1998 to 343 in 1990 (Figure 1). Numbers of older (2nd- and 3rd-year) plants also varied dramatically among years, from one plant for plots A, B, and C combined in 1992 to 34 plants in 1991 (Figure 1). Emergence was concentrated in May, especially, and June, but continued at a low level through October (Figure 2).

Of the 1352 marked seedlings, 53% survived until the end of

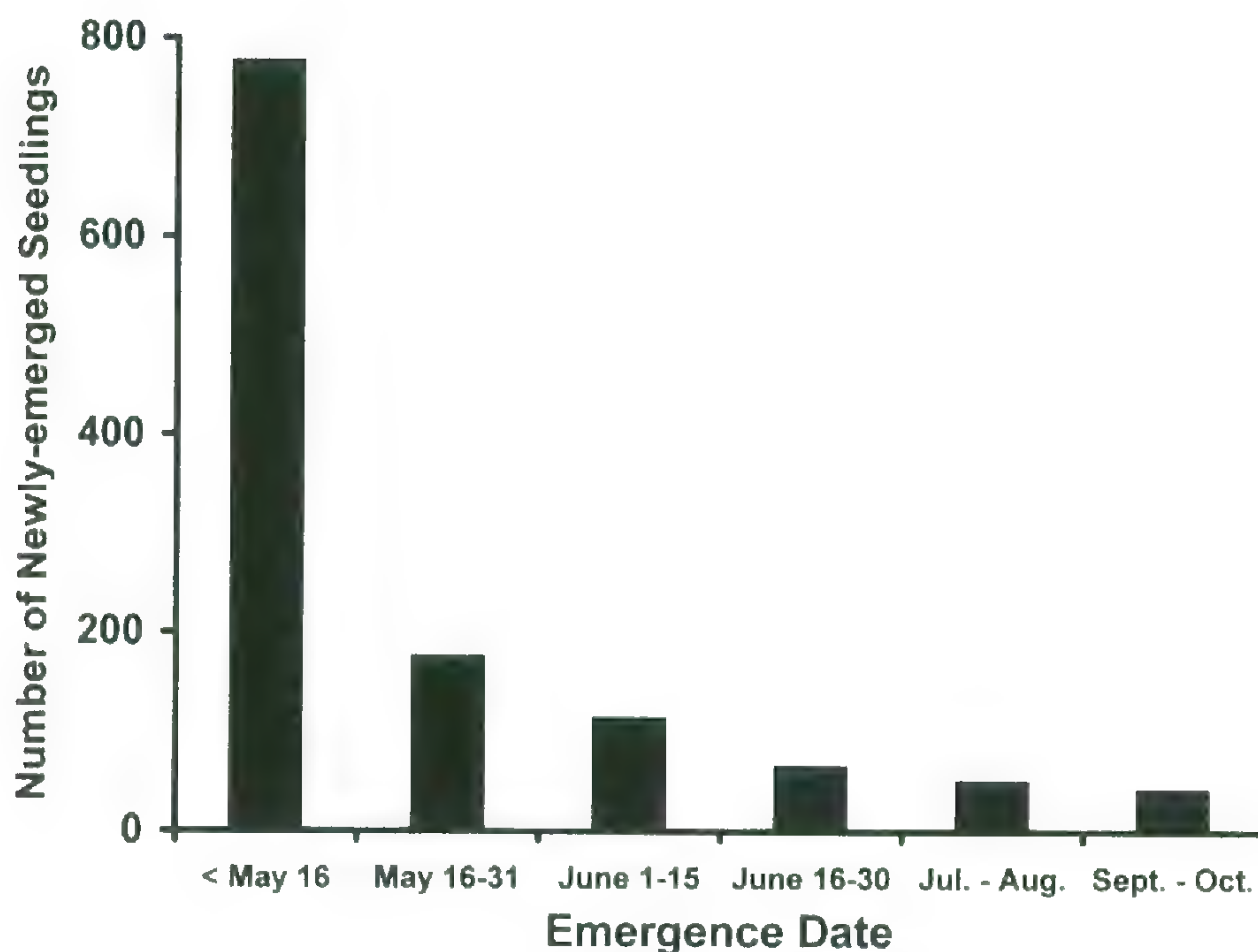


Figure 2. Numbers of newly emerged seedlings at different times of the year. Data are combined for plots A–D and for years 1990–1998.

the first growing season and 7% survived their first winter and produced at least one leaf the following year (Figure 3). Of the 98 plants surviving their first winter, 51% flowered during the second year and subsequently died, 30% died during their second year without flowering, and 14% died during the subsequent winter. The remaining 5% did not flower during their second year, but survived to their third year. Of these five individuals, three flowered and died during their third year and two died without flowering. In all, 53 of the 1352 marked individuals flowered at some time, 50 (94%) in their second year and three in their third year.

Yearly differences in survivorship. Survival of seedlings through their first growing season and first winter varied considerably from year to year (Figure 4). Survival of seedlings to the end of their first year varied from 5.5% ($n = 109$) in 1995 to 65.7% ($n = 201$) in 1996. Overwinter survival ranged from 0.0% ($n = 59$) in 1991 to 21.3% ($n = 150$) in 1992. G tests for independence of year and survival revealed significant departures from independence both for seedling survival during the first growing season ($G = 148.48$, 8 df, $P < 0.001$) and the first winter

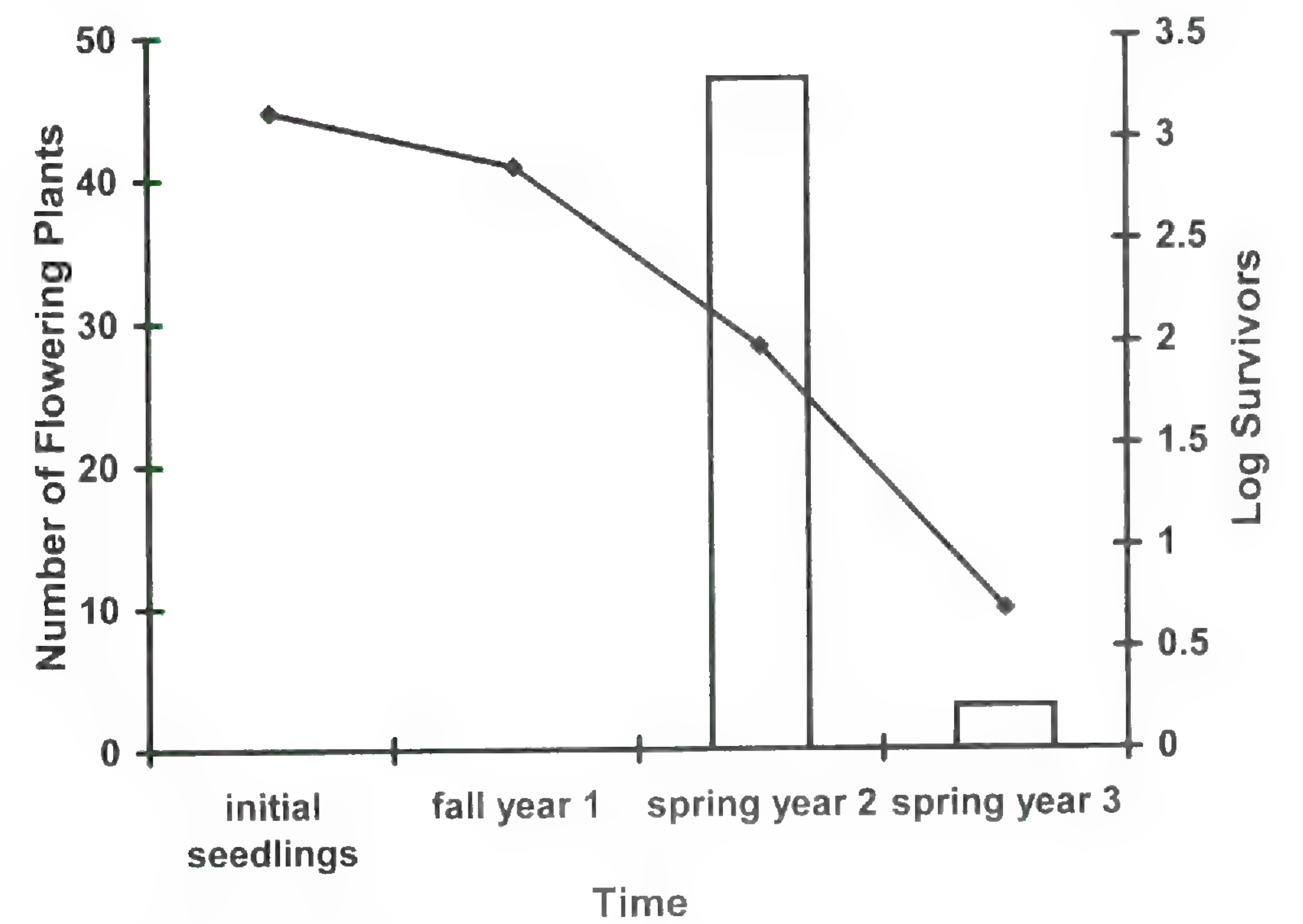


Figure 3. Survival and flowering of 1352 plants marked as seedlings in plots A–D during the years 1990–1998. Survivorship for years 2 and 3 was measured at the beginning of the year. No plants survived to year 4.

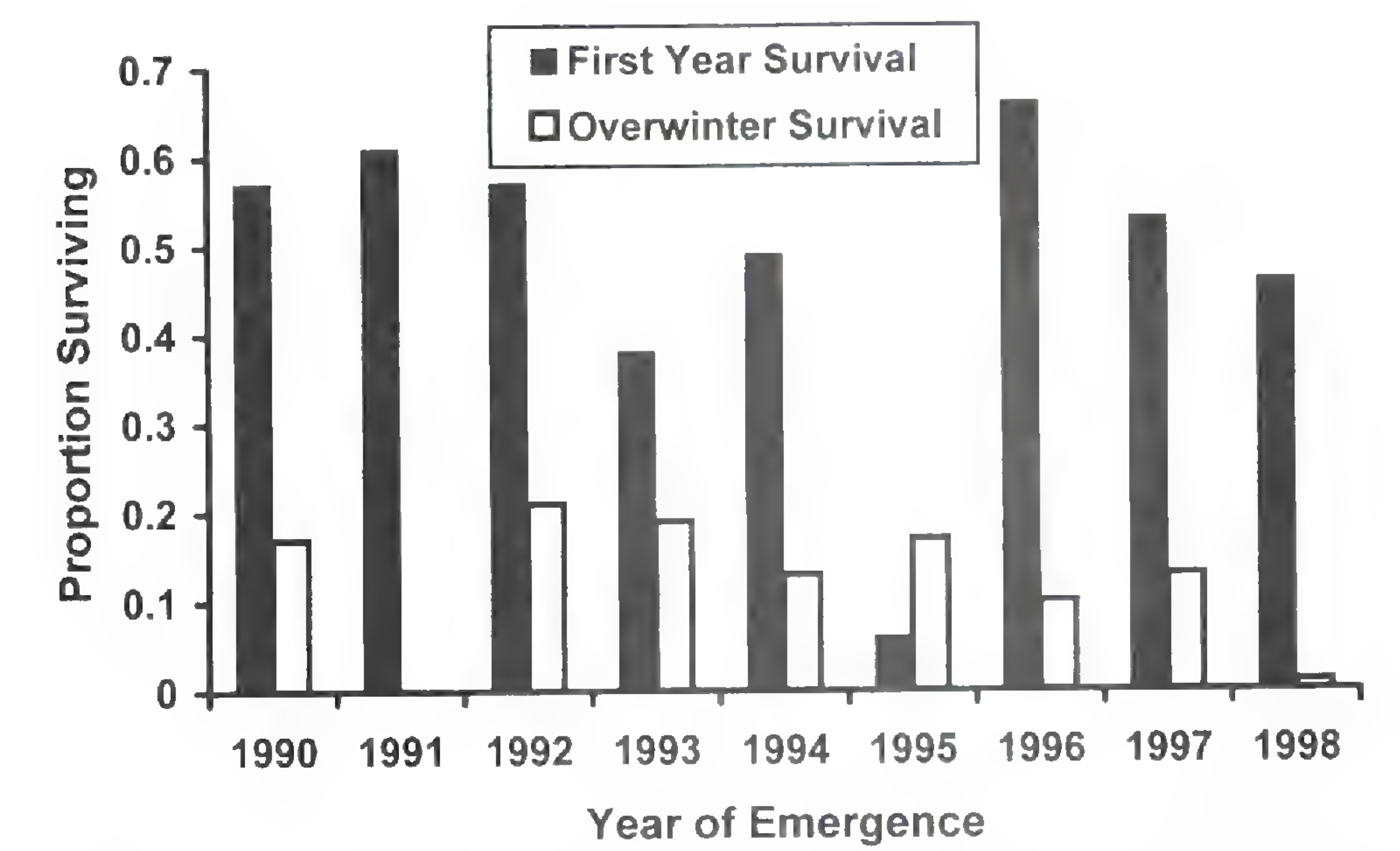


Figure 4. Yearly variation in survival of seedlings emerging in nine years. Data for plots A–D are combined. Overwinter survival is the proportion of plants alive at the end of their first year that survived to spring of the following year.

($G = 44.46$, 4 df, $P < 0.001$). The second analysis has fewer degrees of freedom than the first because it excludes four years of data for which the expected values were below 5.0.

The yearly differences in survival seem in part to reflect prevailing weather conditions, especially precipitation during the summer, and temperature and snow depth during the winter. Survival of seedlings to the end of their first year was positively correlated (though not significantly so, $P > 0.05$) with the amount of precipitation in May ($r = 0.46$), June ($r = 0.57$), and August ($r = 0.36$), but not in July ($r = -0.15$). Survival was, however, significantly correlated with the amount of precipitation in May–July and May–August ($r = 0.68$, 0.74 , respectively, $P < 0.05$). The lowest rainfall for any of these months in the nine years of the study was in June of 1995, when only 3.8 cm of rain fell, 42% of the June average. Over 94% of seedlings died by the end of this year, compared to a nine-year average mortality of 52%.

Overwinter survival of plants alive at the end of the first growing season was positively correlated with total winter snowfall ($r = 0.52$), although not significantly so ($0.20 > P > 0.10$). The winter with greatest survival was 1992–93, which also had a greater snowfall than any winter in the preceding century (3.1 m). If exposure to harsh winter conditions reduces survival, it would seem that a combination of low winter temperatures and minimal snow cover would be more highly correlated with winter mortality than snow cover alone. This is suggested by the nearly significant negative correlation ($r = -0.64$, $0.10 > P > 0.05$) between survival and the number of winter days with both temperatures below -12°C (10°F) and less than 2.5 cm (1 in.) of snow cover. The winter with the lowest survival (1991–92, 0% survival) also had the largest number of such cold days with bare ground (15, compared to 1–7 in other years).

The substantial variation in numbers of seedlings emerging in different years caused the density of seedlings to vary dramatically among years and plots (range = 1–191/m²). This density was not, however, related to survival or flowering. Correlation coefficients between seedling density and survival to the end of the first year, overwinter survival, and proportion of overwinter survivors that flowered were 0.23 ($n = 31$), -0.05 ($n = 29$) and 0.45 ($n = 15$), respectively.

Performance of seedlings. Emergence date was strongly as-

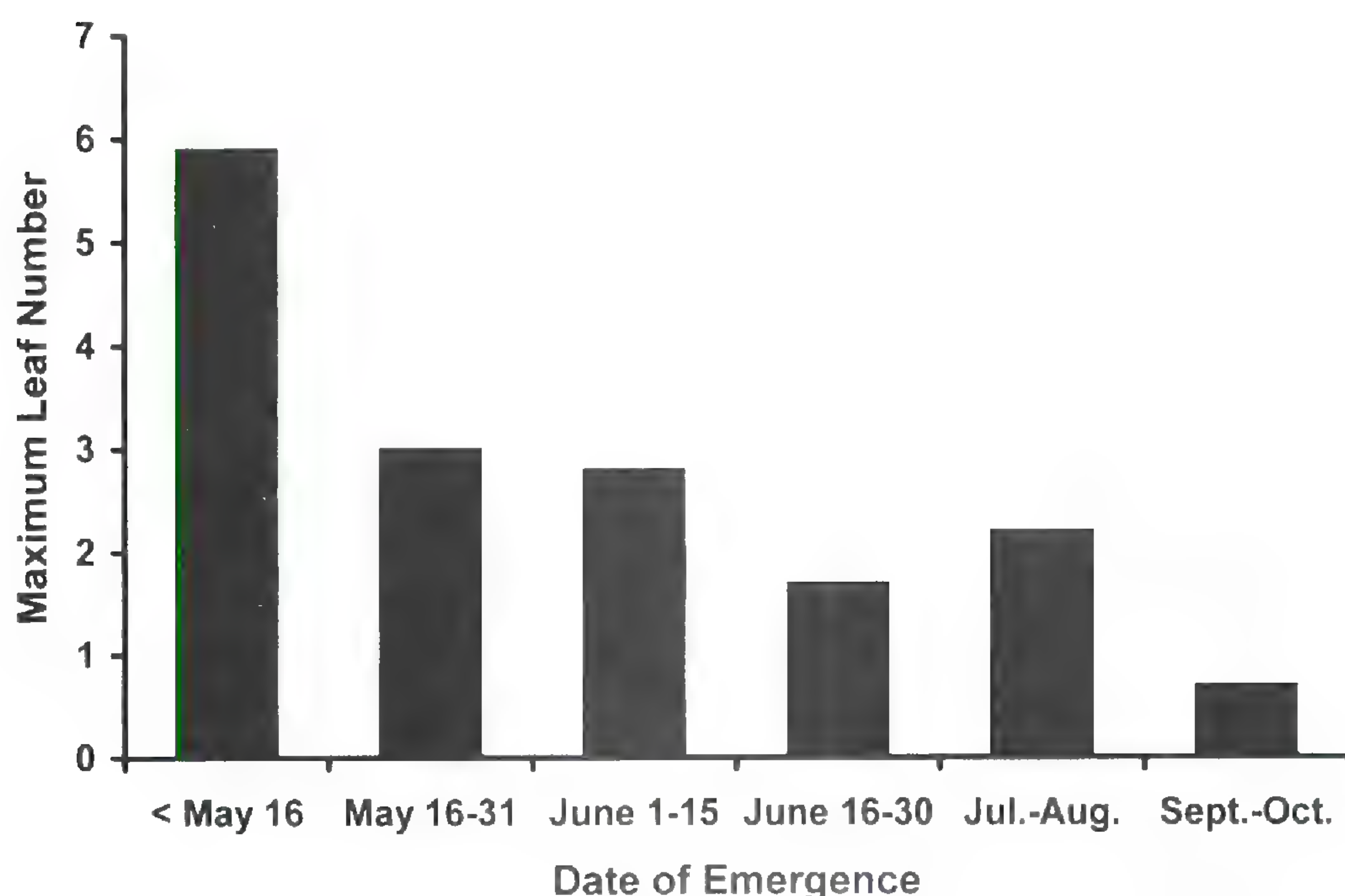


Figure 5. Average maximum leaf numbers produced during their first year by plants emerging at different times of the year.

sociated with the size (as represented by maximum leaf number) attained by first year plants, with their likelihood of surviving to the end of the first growing season, and with the numbers of flowers that they produced. Plants emerging in late April and the first half of May bore an average maximum of 5.9 leaves during their first season, while the average maximum number for the other time intervals was no more than half this number (Figure 5). Plants emerging on or before May 15 had a 56% chance of surviving to the last census date of the year, while the probability for those emerging after May 15 was 0.36. This latter figure was inflated by the high survival of seedlings that emerged in September and October (0.93), reflecting the fact that many of them needed to survive for only 2–3 weeks to live to the end of the growing season.

Plants surviving to the end of the first season had a slightly greater chance of surviving the winter if they emerged on or before May 15 than if they emerged later in the year (18% vs. 11%; $G = 4.46$, 1 df, $P < 0.05$). However, if seedlings emerging in September and October are excluded, the survival of late-emerging seedlings increases to 14%, which is not significantly different from 18% ($G = 1.20$, 1 df).

Of plants surviving to year two, a much greater percentage of those that emerged as seedlings by May 15 flowered than did those that emerged after that date (62% vs. 17%; $G = 13.14$, 1 df, $P < 0.001$). Furthermore, among plants that flowered, those from early-emerging seedlings ($\leq$ May 15) produced over three times as many flowers as late-emerging seedlings (18.7 vs. 5.0; SE = 2.59, 1.67; $n = 48, 5$). This difference between means is significant based on log-transformed data ($t = 3.07$, $P < 0.01$, 51 df).

Plant size attained during a plant's first year influenced the probability of overwinter survival and flowering. Plants alive at the end of their first year and with a maximum leaf number of 3–9 had a 16% chance of surviving the winter, compared to an 8% chance for plants with both fewer (0–2) and more (10+) leaves (G-test for independence, $G = 13.42$, 2 df, $P < 0.01$). Among plants surviving to year two, those bearing 0–2 leaves in their first year had a 33% chance of flowering, compared to a 54–60% chance for plants with 3–9 and 10+ leaves, though the sample sizes were too small to test for independence. Among plants that flowered, the maximum leaf number showed a modest but significant correlation with flower number ($r = 0.41$, $n = 53$, $P < 0.05$).

Substrate depth had a modest but significant effect on seedling survival to the end of the first growing season, with seedlings occupying substrates of intermediate depth (3 cm) having the highest survival (G-test for independence, $G = 15.18$, 5 df, $P < 0.001$; Figure 6). Substrate depth had no effect on overwinter survival of those plants surviving to the end of the first growing season ($G = 2.92$, 4 df, ns), nor on the flowering of those plants surviving until the start of the second growing season ($G = 6.50$, 4 df, ns).

Seed demography. Of the 408 seeds sown into the 12 seed demography plots, 105 emerged within six years, the majority in the year after sowing (Figure 7). At the conclusion of observations, 74% of the original seeds had not emerged, having either died or remained in the soil seed bank. No seedlings were observed within 1.5 m of the marker stakes except for those within 0.3 m of the stakes and presumably sown by me. Thus there is no evidence that the results were confounded by the presence of a naturally occurring seed bank.

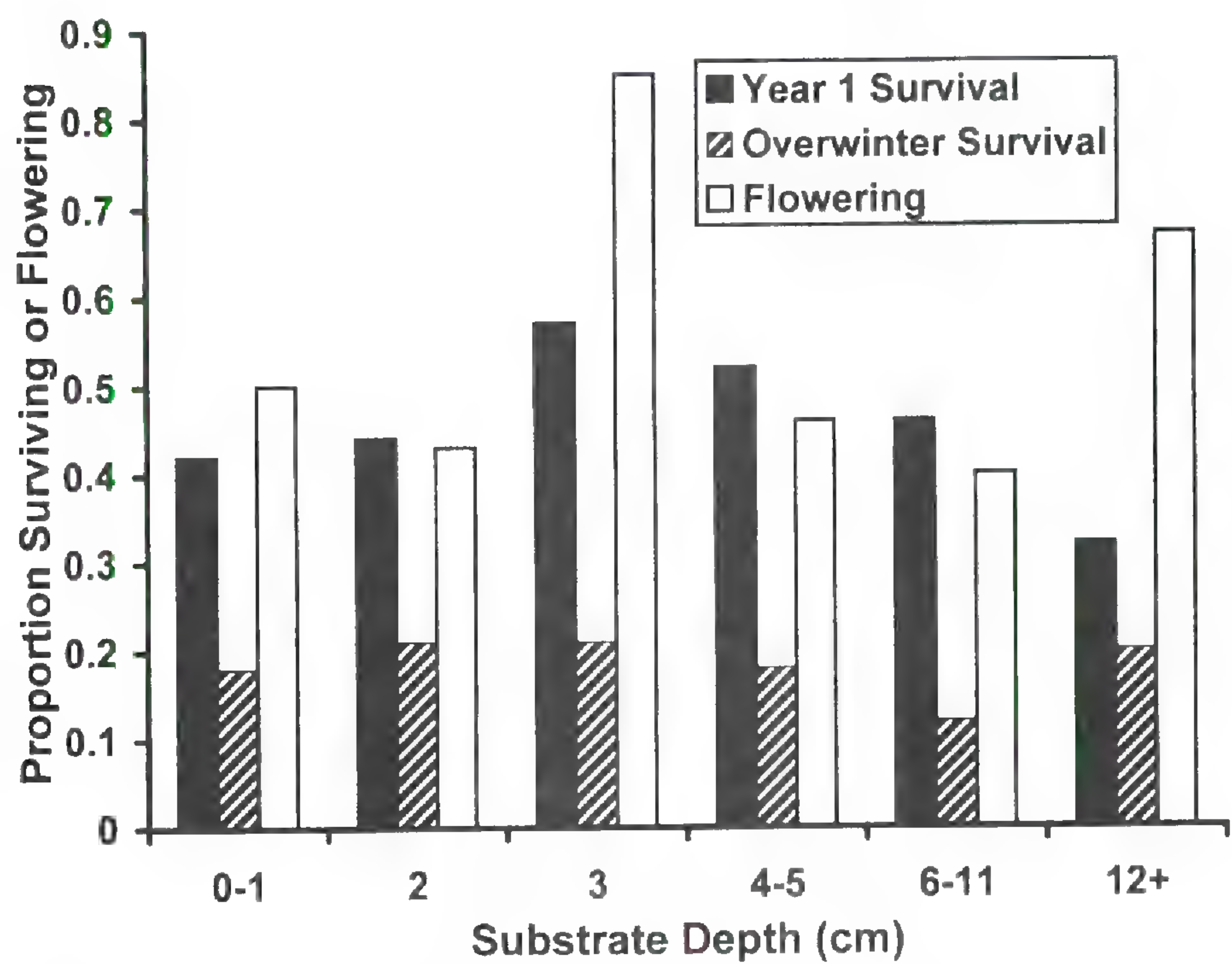


Figure 6. Influence of substrate depth on proportion of plants surviving and flowering. Proportions are calculated as in Figure 7. Data are combined for plots A–D.

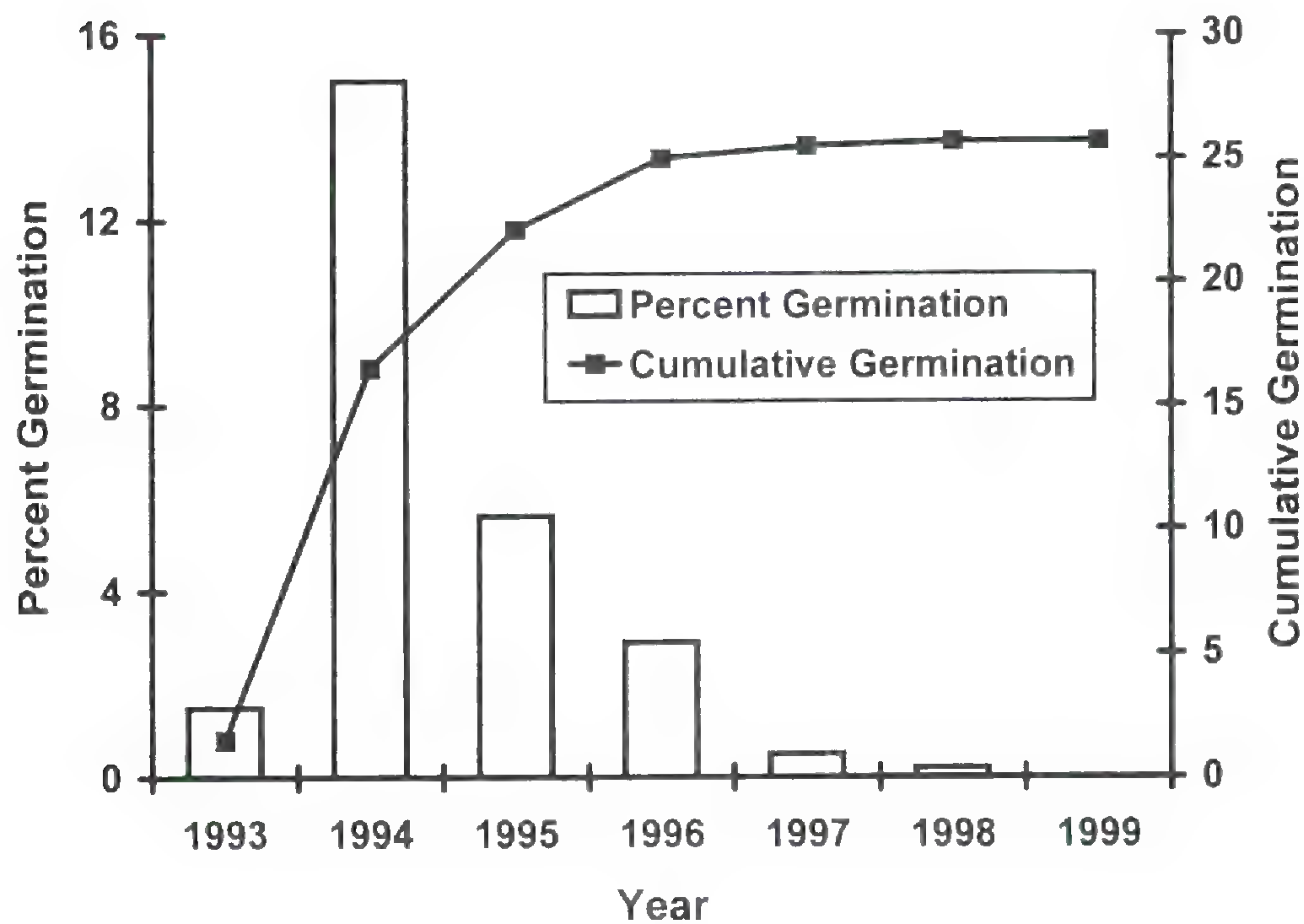


Figure 7. Temporal pattern of emergence of 408 seeds sown in 12 plots during the summer of 1993.

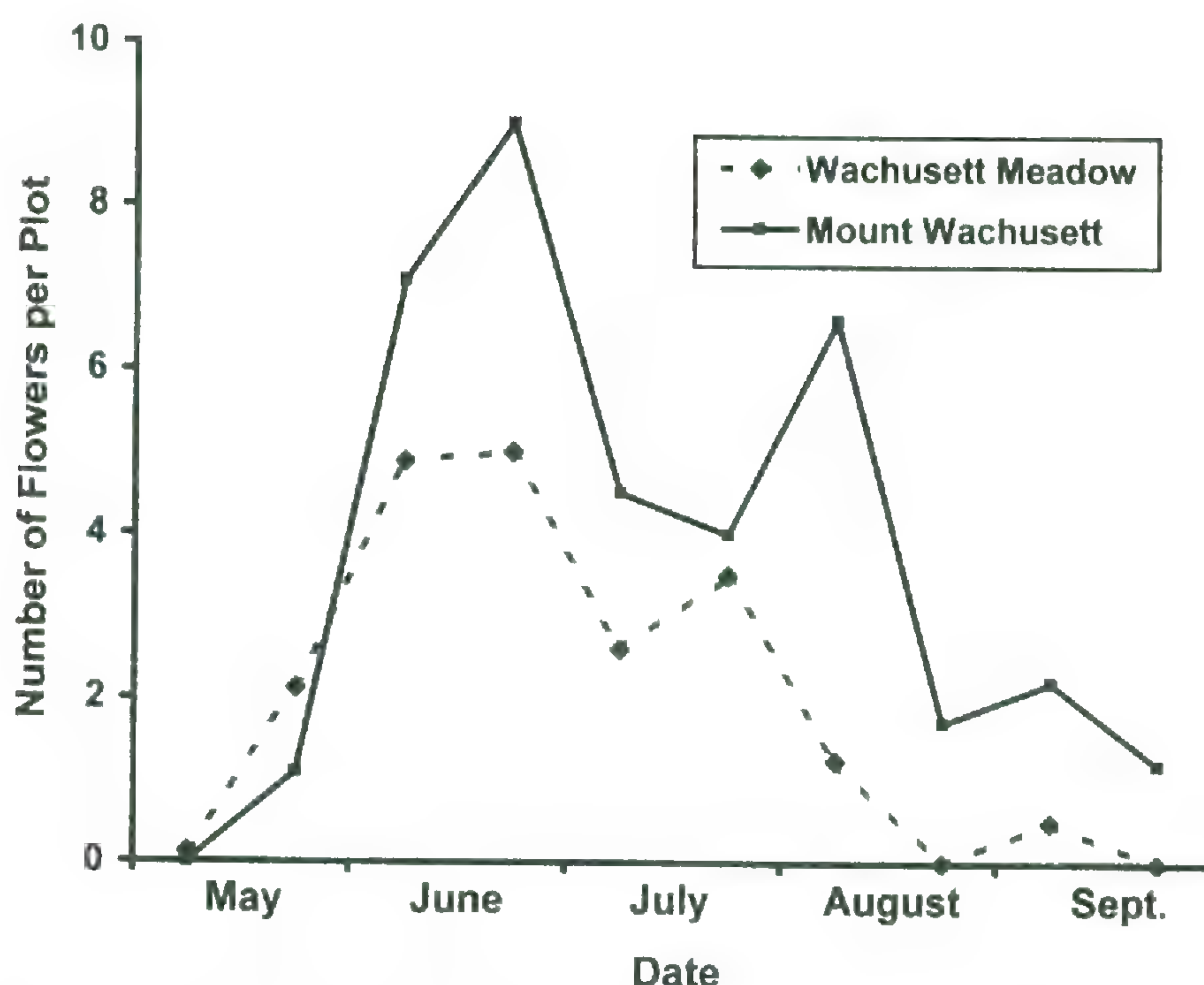


Figure 8. Flowering phenology of plants in plots A and B at Wachusett Meadow and C and D at Wachusett Mountain. Data from 1990–1998 are combined.

Reproductive biology. Flowering at the study sites began in mid May, peaked in June, and gradually declined through September (Figure 8), with an occasional flower as late as November.

Patterns of floral development and pollinator visitation were consistent with a high incidence of self-pollination. Flower buds enlarged to a size of about 9 mm long $\times$ 3.5 mm wide at which time the sepals separated, revealing the underlying pink corolla. Flowers usually opened overnight, with petals initially forming a cylinder around the sexual parts, and then flaring to become perpendicular to the floral axis. Fully open flowers were about 15 mm in diameter. The unopened anthers were initially pressed against the pistil and the stigmatic lobes were appressed. As the petals became fully open, the anthers moved centripetally and the lobes of the stigma separated. The stigma was presumably receptive at this time, making the flowers slightly protogynous. By mid to late morning, the five anthers of one whorl moved towards the pistil and dehisced. The anthers at this time were in contact with the stigmas and above them, covering most or all of the stigmatic surfaces with pollen. The anthers of the second whorl moved

inward and dehisced at midday or in the early afternoon. The opening of anthers in this whorl was less synchronous than the opening of anthers in the first whorl, with dehiscence of successive anthers occurring over a period of several hours, or even on successive days. The stigmatic lobes gradually diverged during anther dehiscence, though on some plants the lobes appeared to close overnight and reopen the next day. At 48 hr. from petal opening, most petals and anthers had dropped, and the stigmatic lobes were furled. Within another 24 hr. the calyx closed. The tip of the stigma extended several millimeters past the tips of the sepals at this time as a result of elongation in the 72 hr. since flower opening. After about three weeks the capsule ripened, and the five seeds were ballistically dispersed.

Pollinators were regular though not conspicuous visitors to woodland herb Robert plants, visiting during the warmer hours of sunny days. A few bumblebees (*Bombus* sp.) paused at the flowers, but contact was limited and pollen transfer was unlikely. The main visitors seen at Wachusett Meadow were small unidentified flies, roughly 9 mm in length, that appeared to be both probing for nectar and collecting pollen. In one 1.5 hr. period on a sunny afternoon, 10 of 35 observed flowers were visited by a fly, corresponding to one visit per flower per 5 hr. Assuming conditions during flowering are suitable for 5 hr. of pollinator activity during each of the two days of a flower's life, the average flower would receive roughly two visits. Visitation rates on inclement days and to isolated flowers are likely to be lower than visitation rates to concentrations of flowers on sunny days.

All flowers examined had ten ovules, although the maximum seed number was five. Anthers from Vermont plants contained an average of 72 pollen grains (SE = 4, $n = 4$) compared to 90 (SE = 7, $n = 5$) for Wachusett Mountain plants and 112 (SE = 7, $n = 5$) for Wachusett Meadow plants. With ten anthers per flower and assuming, as did Cruden (1977), an effective ovule number of five, the pollen/ovule ratios at these sites are 144, 180, and 224, respectively.

Hand pollinations revealed that emasculated plants rarely set fruit (9% of pollinations), while fruit set from self-pollinated, cross-pollinated, and unmanipulated flowers was high (96%, 96%, and 88%, respectively; $n = 23$ –24 in each treatment). Isolated plants in the greenhouse also had high fruit and seed set.

DISCUSSION

Life cycle patterns. Herb Robert at my study sites can be described as a facultative biennial (*sensu* Kelly 1985), or as a short-lived, monocarpic perennial. No plant flowered in the same (calendar) year it germinated and no plant survived to the year after it flowered. Over 90% of reproductive individuals flowered in their second year. The designation "winter annual" is inappropriate for these plants as they germinate mostly in the spring, and few if any reproductive individuals live for less than 12 months. References to the species as an annual in North America (Fernald 1950; Gleason and Cronquist 1991) are also incorrect for central Massachusetts plants. Geographic variation in life cycle pattern in North America is possible given the apparent variation in this characteristic among herb Robert populations in Europe (Baker 1956; Falinska and Piroznikow 1983 and references therein; Yeo 1973). Furthermore, other monocarpic species are known to exhibit an annual life cycle in warm regions and a facultative biennial life cycle in colder areas (Kalisz and Wardle 1994; Lacey 1988; Reinartz 1984).

The biennial habit is rare. Hart (1977) and Bender and Baskin (1994) used theoretical models to account for rarity. While the models differ in important details, both conclude that biennials compete successfully against plants with other life cycles only within a narrow range of juvenile and adult survivorship values. The predicted ratio of these two survivorship values must be in the vicinity of 10^{-4} according to both models. In the present study, if the juvenile period extends from seedling emergence to the end of the first winter and the adult period extends from the end of the first winter to the end of the second winter and is considered only for individuals that do not flower (which inevitably results in death), the relevant survival rates are 0.07 and 0.10. These produce a ratio of 0.7, several orders of magnitude greater than predicted, suggesting that these models do not capture some key factors influencing the evolution of the biennial habit.

Several workers have commented on the habitats in which biennials are expected to occur. Hart (1977) predicted that biennials should be especially common in habitats that are neither open nor closed (e.g., midsuccessional habitats and woodland gaps). Hart further suggested that the biennial habit is appropriate for ex-

exploiting sites with intermittent resources. Schaffer and Gadgil (1975) argued that short growing seasons should favor biennials over annuals because the latter will not have time to procure enough resources for reproduction. In a similar vein, Schat et al. (1989) suggested that bienniality is advantageous in allowing production of a large stem in a short time. They contend that this is especially important in species wherein seed production is determined largely by multiple repetition of architectural units within the plant. Several workers have suggested that biennials are particularly common in early-successional habitats, disturbed habitats, and habitats unoccupied by potential competitors (Kelly 1985; Meijden and Waals-Kooi 1979; Schaffer and Gadgil 1975; Silvertown 1984; Threadgill et al. 1981). However, in an analysis of three floras, Hart (1977) reported that roughly half of the biennials were found only in natural habitats (i.e., those with minimal human influence).

Three categories of biennials were recognized by Meijden et al. (1992): transient, fugitive, and persistent. Species in the first two groups occupy disturbed or changing habitats, have short-lived populations, and produce many seeds. Persistent biennials have more persistent but fluctuating populations and relatively few seeds. All species they described in the persistent category occupy chalk grasslands. Herb Robert fits the profile of a persistent biennial reasonably well, though it is necessary to expand the habitat description beyond grasslands, perhaps to stable or closed habitats. Other woodland biennials or monocarpic perennials that might be categorized as persistent biennials include *Arabis laevigata* (Muhl.) Poiret, *Campanula americana* L., *Frasera caroliniensis* Walter, *Hydrophyllum appendiculatum* Michx., *Phacelia bipinnatifida* Michx., and *Synandra hispidula* (Michx.) Britton (Baskin and Baskin 1988; Bloom et al. 1990; Morgan 1971; Threadgill et al. 1981).

Survival and mortality. Twenty-six percent of hand-sown seeds emerged within 6 yr. of sowing. Survival of dispersed seeds may be higher than this if the seeds remain viable for longer than 6 yr. These figures must be interpreted cautiously since I cannot be sure that the habitats into which the seeds were sown were identical to those into which seeds are dispersed naturally.

Emergence of seedlings was heavily concentrated in early spring. The greater success of early- than of late-emerging seed-

lings could reflect the greater availability of light, water, or nutrients early in the season, or simply the longer growing season available to early-emerging plants. The pattern of emergence seen in this study seems to differ from that in some European populations of the species. In England, Roberts and Boddrell (1985) found germination to be spread more evenly through the growing season. However, by cultivating the experimental plots three times during the year, these authors may have promoted additional germination by exposing buried seeds to light. In Poland, Falinska and Piroznikow (1983) reported that groups of new offspring appeared several times during the year, though they did not indicate whether these were three entirely distinct cohorts, or parts of a continuum of germinations divided for convenience of study. The plants emerging in spring, summer, and fall differed in several aspects. As is true in my study, seedlings emerging in the spring had the highest survival rates and likelihood of flowering. Plants from the vernal cohort were invariably biennial, whereas those of the aestival cohort flowered during either their second or third year. Plants from the autumnal cohort were few in number and often did not survive to their second year.

In the present study, half of emerging seedlings did not survive to the end of the first growing season, and 87% of survivors died during the succeeding winter. General levels of mortality during both the growing season and the winter appeared to be related to weather conditions. High summer mortality was associated with low rainfall and high winter mortality with cold temperatures and little snow cover. Similar influences on winter mortality were noted for another forest biennial, *Hydrophyllum appendiculatum* (Morgan 1971). In two years, overwinter mortality decreased from 91% to 17%, with the former figure from a winter when "a period of warm temperatures [was] followed by record low temperatures with little snow cover". Short-lived plants might be especially susceptible to harsh winter conditions because they have less chance than perennials to establish a deep root system.

Two factors were related to performance of individual seedlings: emergence date and substrate depth. Plants emerging before the middle of May grew larger during their first year and had a greater chance of surviving to the end of the first growing season than did later-emerging plants. Their overwinter survival was, however, little affected by emergence time. Effects of germination time on the performance of plants are well known (Jones et al.

1997; Kalisz 1986). In most spring-germinating species, early emergence is beneficial (Miller 1987), although this may not be the case in fall-germinating species (Kalisz 1986).

Previous studies also have shown strong influences of vegetative plant size on survival and reproductive output, with large plants inevitably doing better than small plants (Gross 1981; Klinkhamer et al. 1987; Werner 1975). Vegetative size of first-year herb Robert plants influenced overwinter survival and apparently also flowering. In contrast to the typical pattern in other species, however, plants of intermediate size were most likely to survive the winter. It is not clear why larger plants did not do better than plants of intermediate size. One possibility is that the leaves (which persist through the autumn) of the largest plants may be found more often by browsing deer (which seemed to be common at both sites) during this season than those of smaller plants, which are better concealed by fallen tree leaves.

Reproductive biology. Herb Robert is highly self-compatible and capable of full seed set in the absence of pollinators. While experimental pollinations used plants from Vermont, it seems likely that Massachusetts plants behave similarly. The occasional fruit set observed in emasculated flowers in the laboratory was presumably due to contamination with pollen, since the small flower size made it difficult to remove the anthers cleanly and pollen grains were occasionally observed on the stigmas of flowers in this treatment.

The actual level of self-pollination in nature is unknown, but probably high. Pollen grains were often observed on stigmas in the early morning before pollinators were seen, and before there was evidence of insect removal of pollen from the anthers. The proximity of anthers and stigmas, and the infrequency of visitors, particularly during the early morning female phase before autogamy occurs, made self-pollination a virtual certainty. Baker (1953) concluded that the species was largely selfed in Great Britain, with “rarely more than 2–3% of outcrossing.”

Other aspects of herb Robert’s floral biology also suggest a predominance of selfing. Compared to its sympatric congener, *Geranium maculatum*, the flowers of *G. robertianum* are small (11–15 mm vs. 32 mm) and the pollen/ovule ratio is low (140–230 vs. 1062; Cruden 1977; Martin 1965). The former range falls between the means of Cruden’s (1977) categories of obligate au-

togamy and facultative autogamy, while the latter lies between facultative xenogamy and xenogamy.

According to reports in the literature, the reproductive biology of herb Robert is somewhat variable. Knuth (1908) reported that unisexual flowers occurred in addition to hermaphroditic ones, although none was observed in the present study. Different observers have reported the flowers to be either protandrous or homogamous (Knuth 1908), in contrast to the slight protogyny observed in Massachusetts plants. Knuth (1908) described the flowers as though cross-pollination was frequent as a result of the protandrous condition of flowers and the projection of the stigmas above the anthers. He further recorded a variety of floral visitors in Europe, including large and small bees, flies, butterflies, and beetles.

In central Massachusetts, herb Robert is predominantly a woodland biennial that grows in thin organic soils on and around boulders. Its survivorship appears to be influenced by summer droughts and cold winter periods with minimal snow cover. These factors are probably associated with the dramatic year-to-year fluctuations in abundance of reproductive plants. Self-pollination may be advantageous in such situations, allowing reproduction when density of reproductive individuals is low. Under such unpredictable conditions, seed dormancy and a seed bank are helpful in insuring survival of some offspring in the face of consecutive bad years. A strict interpretation of the species' life cycle in terms of these environmental conditions seems inappropriate because other species in the same vicinity exhibited other life history patterns. Nevertheless, herb Robert was more likely to occupy thin litter over rocks than other species. Plants in this microhabitat may be at a higher risk of mortality than species in deeper soils, and this may reduce the advantage of allocating resources to future reproduction, favoring a biennial life cycle to a perennial life cycle. The absence of an annual life cycle might reflect the difficulty in accruing sufficient resources for reproduction in a single growing season in the low light conditions of the forest floor.

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NEW ENGLAND NOTE

TRIGLOCHIN MARITIMA (JUNCAGINACEAE)
DISCOVERED IN VERMONT

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Triglochin maritima L. VERMONT: Orleans Co., East Charleston, Clyde River, 2.25 km downstream from Orleans Co. line, intermediate fen floating in broad area of river, 3 Sep 1998, *Lapin 98088 & Engstrom* (VT); 15 Sep 1998, *Lapin 98113 & Engstrom* (VT).

Triglochin maritima (common arrow-grass) is a circumboreal and north-temperate plant common in brackish water of coastal marshes and shores, but also known from inland freshwater marshes and shores, bogs, and swamps (Crow and Hellquist 1982; Fernald 1950; Gleason and Cronquist 1991; Hulten 1968; Seymour 1982). The range of the species in New England as noted by Seymour (1982) is “Me.: Aroostook Co., Hampden, Skowhegan, Washington Co. along seacoast to Ct., Fairfield Co., not B.I.” (Block Island, Rhode Island). Crow and Hellquist (1982) note that the species was last found inland (in New England) in 1935 in Maine. The species was not previously known to occur in Vermont.

On 3 September 1998, in the course of inventory work of the wetlands of the Lake Memphremagog watershed, the authors were exploring wetlands associated with the Clyde River. In a broad, slow-water stretch of the river, expansive graminoid wetlands were bordered by red maple-northern white cedar (*Acer rubrum*–*Thuja occidentalis*) swamp, parts of which had been inundated due to construction of a bridge over the river. The upper Clyde River is in the bedrock-contact zone where the Gile Mountain formation meets granitic rocks of the New Hampshire plutonic series (Doll 1961). The Gile Mountain formation is predom-

inantly quartz-muscovite phyllite or schist, but it does include interbedded calcareous mica schist, and quartzose and micaceous crystalline limestone. A wide swath of the Waits River formation, which contains much siliceous crystalline limestone, occurs west of these wetlands. Glacial drift from the limestone likely enriches the soils in this portion of the Clyde River valley. Many of the wetlands there show a pronounced influence of calcareous enrichment in soils and seepage waters.

We maneuvered our canoe through patches of cattail (*Typha latifolia* L.) and pickerelweed (*Pontederia cordata* L.) and stepped out onto a floating mat dominated by *Carex lasiocarpa* Ehrh. and *Myrica gale* L. Upon this soggy, floating mat of sedge peat, we happened upon a 45 cm tall, fruiting stem of *Triglochin maritima*. Searching the immediate area, we discovered in total three fertile and three vegetative stems in a 100 m² area. We later returned to the site to better quantify the population and to characterize the ecosystem in which it occurred. Our final count for the 1998 season was 27 fruiting stems in a one-half hectare area. Leaves had largely withered this late in the season, thus we were unable to count vegetative individuals. Other associated plant species included *Menyanthes trifoliata* L., *Dulichium arundinaceum* (L.) Britton, *Potentilla palustris* (L.) Scop., *Vaccinium macrocarpon* Aiton, *Bidens cernuus* L. var. *minimus* (Huds.) Pursh, *Cicuta bulbifera* L., *Eriocaulon aquaticum* (Hill) Druce, *Rhynchospora alba* (L.) Vahl, *Triadenum fraseri* (Spach) Gleason, *Utricularia gibba* L., *Cladium mariscoides* (Muhl.) Torr., and *Salix pedicellaris* Pursh. The latter three species are rare or uncommon in Vermont. *Triglochin maritima* grew on both floating and non-floating parts of the fen; the peat was poorly decomposed and ranged from 1 to 3 m deep.

Continuing the inventory work in the vast wetland complex, we explored the wide open, glade-like landscape of meandering river, sedge meadow, intermediate fen and shrub swamp. We know of no similar landscape in Vermont. Despite hours of searching many hectares of sedge meadow and fen, we discovered no additional plants of *Triglochin maritima*.

The new plant discovery and additional information about the wetlands in this portion of the Clyde River were later useful in easement planning for a farmland conservation project. Although a small part of the wetland ecosystem was impacted by bridge construction some years ago, this portion of the Clyde River and

the associated wetlands remain a high-quality natural area that deserves protection and appreciation.

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NOTE

FIVE NEW COMBINATIONS IN THE GENUS *MORELLA*
(MYRICACEAE) FOR NEOTROPICAL SPECIES

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Major variation within the small family Myricaceae is extensive and these fundamental discontinuities have been pointed out from the earliest days of systematic botany. In spite of the early recognition of the strikingly obvious divisions within this family of perhaps sixty species, the prevailing practice has been to recognize very few genera and throughout most of post-Linnean times not more than the genus *Myrica* itself. A very large percentage of the intrafamilial variation is represented in northeastern North America and wherein a second genus (*Comptonia* L'Hér. ex Aiton) was finally adopted by Fernald (1938: 379, 380, 410, 412, 482; 1950: 525). Gleason (1952: 24) saw fit to include *Comptonia* and *Gale* Duhamel within *Myrica*, although he did provide, perhaps reluctantly and certainly nomenclaturally incorrectly, the alternate names under two additional generic names. Increasingly, within the past three decades or so, the trend has been to accept three genera in addition to the relatively unknown New Caledonian monotypic genus *Canacomyrica* Guillaumin. These genera are *Myrica* L. (Lectotype: *Myrica gale* L.), *Morella* Lour. (Lectotype: *Morella rubra* Lour.), and *Comptonia* [Type: *Comptonia asplenifolia* (L.) L'Hér. ex Aiton; = *Comptonia peregrina* (L.) J. M. Coult.].

All members of the Myricaceae known from Mexico, Central America, South America, and the West Indies bear waxy drupes and hence are species of *Morella*. I have recently examined a very considerable number of collections from Mexico and Central America from 15 herbaria (A, ARIZ, CAS, CONN, DUKE, F, GH, LL, MICH, MO, NY, TEX, UC, US, WIS) and find need for the following combinations in the genus *Morella*. Study of the West Indian representatives has been initiated and has already shown that cer-

tain combinations are needed now. It seems certain that others will also be required, but the necessary Antillean study has not been completed so they will be published later.

The last monographer of the Myricaceae, Chevalier (1901) actually recognized the same generic groupings that are currently being adopted. However, Chevalier in effect typified the Linnean genus by *Myrica cerifera* L. instead of by *Myrica gale* and as a consequence the largest cluster of species was treated as the genus *Myrica* instead of forming the genus *Morella*. The lectotype of the genus *Myrica*, as noted in the first paragraph, is *Myrica gale*, designated in Britton and Brown (1913: 584). This is the only species native to Sweden and the only species familiar to Linnaeus in its natural setting. Consequently, *Myrica gale* was the species best known to Linnaeus and a fitting lectotype for the genus. Killick et al. (1998) have recently transferred the African representatives from *Myrica* to *Morella* and Parra-Osorio is currently preparing a manuscript transferring the South American representatives to *Morella*. Wilbur (1994) dealt with the North American representatives of *Comptonia*, *Morella*, and *Myrica* and concurred with the unpublished dissertation by Baird (1968). Verdcourt and Polhill's proposals (1997) to conserve the generic names *Myrica* and *Gale* with the conserved types *Myrica cerifera* and *Gale belgica* Dumort, were rejected by the Committee for Spermatophyta as reported by Brummitt (1999), a conclusion that was approved by the most recent Botanical Congress.

Mexico and Central America:

- 1) ***Morella phanerodonta*** (Standl.) Wilbur, *comb. nov.*; Basionym: *Myrica phanerodonta* Standl., J. Wash. Acad. Sci. 17: 164. 1927.
- 2) ***Morella pringlei*** (Greenm.) Wilbur, *comb. nov.*; Basionym: *Myrica pringlei* Greenm., Proc. Amer. Acad. Arts 41: 236. 1905.
- 3) ***Morella pubescens*** (Humb. & Bonpl. ex Willd.) Wilbur, *comb. nov.*; Basionym: *Myrica pubescens* Humb. & Bonpl. ex Willd., Sp. Pl. 4: 746. 1806.

West Indies:

- 4) ***Morella holdridgeana*** (Lundell) Wilbur, *comb. nov.*; Basionym: *Myrica holdridgeana* Lundell, Contr. Univ. Michigan Herb. 7: 5. 1942.

- 5) **Morella picardae** (Krug & Urb.) Wilbur, *comb. nov.*; Basionym: *Myrica picardae* Krug & Urb., Bot. Jahrb. Syst. 15: 359. 1892.

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NEW BOOKS

Coastal Plants from Cape Cod to Cape Canaveral by Irene H. Stuckey and Lisa Lofland Gould. Expected publication date: March 2000. 304 pp. 129 color photographs. ISBN 0-8078-2582-4 \$29.95 (hardcover), \$14.94 (softcover). The University of North Carolina Press, Chapel Hill, NC.

Flora of Florida, Volume I: Pteridophytes and Gymnosperms by Richard P. Wunderlin and Bruce F. Hansen. 2000. 365 pp. 76 black and white figures. ISBN 0-8130-1805-6 \$49.95 (hardcover). University Press of Florida, Gainesville, FL. [1-800-226-3822; <http://www.upf.com>]

Vascular Flora of Worcester, Massachusetts by Robert I. Bertin. 2000. 155 pp. 2 maps. \$15.00 (softcover, spiral bound), \$5.00 (CD-ROM). Special Publication of the New England Botanical Club, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138-2020.

NEBC MEETING NEWS

September 2000. Les Eastman of Greene, Maine, spoke on the “Naturalists of New England.” Les has been fascinated by the lives of New England naturalists since his teenage days as a rock-hunter. His years of research have brought him to a rich assemblage of personal histories, and he endeavored to share with us a glimpse of these past lives. Any treatment of New England naturalists and natural history includes our mountains. A white man first explored Maine’s highest mountain, Katahdin, in 1804, the same year that President Jefferson sent Lewis and Clark on their expedition to find a passage to the Pacific. Charles Turner of Scituate, Massachusetts, returned from Maine with the first descriptions of the alpine vegetation of Katahdin. In the years to follow, the slopes and summits of Mt. Washington and Mt. Katahdin were further explored by the likes of William Peck (*Geum peckii*), Francis Boot (*Prenanthes bootii*), and Edward Tuckerman. Peck was the first person hired to teach natural science at Harvard. Boot was the world’s expert on *Carex*, and Tuckerman taught at Amherst.

One of the region’s first field naturalists was the Englishman John Josselyn, who traveled to the provinces of Maine in the 1760s upon the instructions of Fernando Gorges, who held the crown leases. Josselyn was based in Saco, Maine, and his *New England Rarities* was brought to light more than a hundred years after its writing. Les introduced us to the likes of Eliza Hamlin, who headed the Gardiner Lyceum—the first incarnation of the University of Maine. Thomas Nuttall traveled to Maine to collect tourmalines for Harvard. John J. Audubon hired a young sharpshooter in Dennysville, Maine, on his way to seek out new birds and mammals in the wilds of Labrador. The Lincoln Sparrow was named in the lad’s honor.

Les presented images of interest and intrigue. Thoreau, the abolitionist, had a wonderful relationship with God-fearing Louis Agassiz, whose Museum of Comparative Zoology at Harvard was funded in large part by southern slave owners. Mainer Edward Sylvester Morse left his native state to study with Agassiz and abruptly left his post at the MCZ when it was discovered that he was carrying on correspondence with Charles Darwin. Morse became the Curator of the Peabody Museum of Salem. Les has an abiding interest in tracking down the scattered remnants of the

old Portland Society of Natural History. The Society's museum was first built in the 1830s, then rebuilt by the great-grandfather of aquatic plant specialist Norman Fassett. The collections of such luminaries as Arthur Stanley Morton, Edward Sylvester Morse, and George Lincoln Goodale were housed at the Portland Society of Natural History. Les has retraced the web of relationships between the naturalists of these far-gone decades in an effort to better understand their work. George Lincoln Goodale wrote the first Catalogue of Maine Plants in 1868, for example, before arranging to bring the world-famous glass flowers to the Peabody Museum at Harvard. Les finished up his presentation with a nostalgic ride down memory lane for Josselyn Botanical Society devotees. Pictures of Merritt Fernald and Kate Furbish riding buckboards in the streets of Fort Kent lent a real sense of historical continuity for all the field botanists in the crowd who have spent time searching for rare plants along the upper St. John River.

Les ended his presentation with a collection of paintings of Mt. Katahdin, beginning with those made by Frederick Church in 1852. Les put great stock in the masters of the 19th century, whether scientists or artists. He lamented the passing of the era of great naturalists, and we were left to imagine that he was quietly urging us to rekindle such broad interest in the diversity and life of our region.

—DON HUDSON, Recording Secretary.

October, 2000. Dr. James Fownes, of the Department of Natural Resources Conservation at the University of Massachusetts at Amherst, spoke on "Productivity, disturbance and management of Hawaiian forests." Hawaii's native plant communities are dominated by relatively few species but occur on an extraordinary range of soil ages and types. Much of Dr. Fownes's research involved studying the relationship between soil formation and forest productivity across a broad gradient of soil ages, using *Metrosideros polymorpha* (Myrtaceae), one of the most common dominant forest trees. He tested various hypotheses concerning changes in nitrogen and phosphorus concentrations and availability in soils, and the relationship of plant productivity (as measured by leaf area, leaf turnover, photosynthetic rates) to soils of varying nutrient concentrations. One of his conclusions is that

Metrosideros is “frugal”—it conserves nutrients when they are at low concentrations or low availability.

A second research project involved *Acacia koa*, a striking native tree with sickle-shaped phyllodes. Koa is a valuable timber tree and heavily grazed by cattle, threatening its persistence. Like *Metrosideros*, it grows across a wide range of ecological conditions. One experiment involved determining the relationship between tree height, basal area, and productivity across a rainfall gradient on Kauai. Dr. Fownes also looked at the response of Koa growth and reproduction to grazing, to determine if there are strategies that allow these threatened trees to co-exist with grazing in buffers to preserves. He found that grazing, if introduced between five and ten years after the establishment of a stand of Koa, allowed trees to persist. Managed grazing, with periodic cattle exclusion for 5 or more years, appears optimistically to provide an integrated land use with conservation benefits.

—LISA A. STANDLEY, Recording Secretary *pro tempore*.

November 2000. Dr. Robert Bertin, Chairman of the Biology Department at the College of the Holy Cross, spoke on “Fifty years of change in the flora of Worcester, Massachusetts.” Robert had something of a mid-life crisis several years ago while assembling his dossier. Would years of investigating sexual systems and plant reproduction survive the cruel knife of history? Would anyone know about his work? Worse yet, would anyone care? So it was that his examination of the flora of Worcester took shape. In a day and age when floristic studies are often overlooked or discounted, Robert recognized the inherent value of such work to colleagues, students, city planners, and conservation-minded citizens. The botanical landscape of Worcester was not very well known, yet the pressure of development was unrelenting. Also, if he undertook the project, he would have ample time in the field—a botanist and ecologist’s dream!

The City of Worcester lies largely in the watershed of the Blackstone River near the geographic center of the state. The western edge of the city sits atop a 1000 ft. escarpment that falls to 300 ft. in the east. Soils are underlain by till and some sorted glacial outwash material. Three bodies of water pre-date European settlement, Lake Quinsigamond, Bell Pond, and parts of Indian Lake. These have been added to by damming during the

past 300 years. Forests, largely comprising black and white oak and hickory, have been reduced in total area and allowed to recover repeatedly over the centuries. The story for wetlands, on the other hand, is grimmer. Whereas 5% of Worcester was wetlands in 1830, less than 1% of it is today. Peat bogs remain in two areas, at Peat Meadow and Broad Meadow Brook. The latter is on land conserved by the Massachusetts Audubon Society. There were perhaps as many as 300 native Americans living in this area when Europeans first passed through in the early 1600s. Native people likely cleared some forest intensively for gardens, while using fire in other places to influence populations of game species. The permanent white settlement commenced in 1713, and the landscape of Worcester has changed dramatically since that time.

Fieldwork on the *Flora* began in 1994 with the collection of records at 77 sites throughout the city. Robert visited these sites, which included ponds, streams, vegetated wetlands, tracts of undeveloped lands, parks, cemeteries, power lines, and railroads to name a few, at different times throughout the year in order to catch plants at their several stages of development. A total in excess of 11,000 records forms the basis of the *Flora*. In addition, Robert gleaned historical information about the flora from the herbaria of Clark University, Harvard University, and the University of Massachusetts at Amherst. All told, 1407 species have occurred within the city limits, of which 1154 were established. Robert has observed 1049 species since 1994. A flora comparable to that of Concord or Nantucket, half the species of Massachusetts are found in Worcester. Over the course of his investigations since 1994, Robert has discovered 83 county records—most waifs and adventives, though a few of these are native species. *Carex* has the most representatives in the flora with 72, followed by *Polygonum*, *Aster* (*sensu lato*), *Panicum*, *Viola*, *Solidago*, and *Juncus*, all with 13–19 species. Three species are state-listed and 6 more are candidates for the watch list. If the herbarium records are to be trusted, 17% of the flora has been lost (129 of 781 native species), which is a measure less than that of Staten Island, Middlesex Fells, and Nantucket, but more than that of Concord.

Robert reviewed the highlights of both the fieldwork and the finished *Flora* with a series of elegant slides. His story of botanizing in the rail yard was particularly compelling. Who would

have imagined encountering plant enthusiasts amidst a group of ironworkers?

Copies of Dr. Robert I. Bertin's *The Flora of Worcester, Massachusetts* are available from the Special Publications Committee, New England Botanical Club, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, MA 02138-2020. The cost is \$15.00 for spiral-bound paper copy and \$5.00 for CD-ROM copy.

—DON HUDSON, Recording Secretary.

CHECKLIST FOR CONTRIBUTORS TO *RHODORA*

Please check items and submit with manuscript.

General Instructions

- Type manuscript on one side only of 8½ inch × 11 inch paper. Leave a 1-inch margin on all sides. Use a standard 12-pitch font type throughout the manuscript, including tables and appendices.
- Do not justify the right margin. Avoid hyphens or dashes at the right margin.
- The manuscript should be fully double-spaced throughout, including title, authors' names and addresses, Literature Cited, appendices, tables, and figure legends.
- Each page of the manuscript; excluding page 1 but including Literature Cited, tables, appendices, and figure legends; should be numbered in the upper right-hand corner.
- Correct accents, umlauts, and other diacritical marks should be included. Where appropriate, multiplication symbol must be used rather than the letter x.
- Only names at the rank of genus and below are italicized or underlined. If underlining is used, do not underline spaces or punctuation.
- Special typefaces (italics, bold) should not be used except where indicated in this checklist.
- Do not italicize common Latin words, abbreviations, or phrases (e.g., et al., i.e., etc.).
- Manuscript should be checked for consistency, especially in matters of abbreviation, names of sites or vegetation types, spelling of names, etc.
- *The Chicago Manual of Style*, most recent edition, is used as a reference in most matters of style. Refer to recent issues of *Rhodora*.
- Assemble the manuscript in the following order: (1) Introductory material, (2) Text, (3) Acknowledgments, (4) Literature Cited, (5)

Appendices, (6) Tables, (7) Figure legends, (8) Figures.

Introductory Material

- **Running head** should be centered, at top of page, in upper and lower case letters. Include author's surname (if two authors use the word "and"; use "et al." for more than two authors), long dash, and short title. Total characters, including spaces, must not exceed 50.
- **Title** should be centered, in upper and lower case. Only the first word of the title and proper nouns should be capitalized. Do not include authors of scientific names. Include family name in parentheses unless genus studied is type for the family.
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- **Abstract** must be one paragraph. The abstract should be a concise statement of intent, methods used, results, and significance of findings. Do not cite references or taxonomic authors, or use and define abbreviations in the abstract. The word "Abstract" should be indented, in all capital letters, followed

by a period, and should appear on the first line of the abstract.

- **Key Words** are used in indexing and should be chosen with that purpose in mind. The title “Key Words” should appear at the left margin, followed by a colon. Only proper nouns should be capitalized.

Text

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- Second-level headings should be indented, bold, upper and lower case, followed by a period, and should appear on the same line as the subsequent text. The text should be written such that additional levels of headings are not used.
- Each figure and table must be cited in the text in numerical order. The word “Figure” must be spelled out. When citing both together, the table should be listed first and a semi-colon used to separate the two (e.g., Table 1; Figure 1).
- Each reference cited in the text must appear in the Literature Cited section and vice versa. Cross-check spelling of author(s) name(s) and dates of publication.
- Literature is cited in the text as follows:
 1. One author: Hill (1982) or (Hill 1982).
 2. Two authors: Angelo and Boufford (1996) or (Angelo and Boufford 1996).
 3. More than two authors: Mathieson et al. (2000) or (Mathieson et al. 2000).
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 5. When more than one paper is cited at a time, they should be listed alphabetically by first author rather than chronologically [e.g., Angelo and Boufford (1996), Hill (1982), Mathieson et al. (2000)].
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 7. Manuscripts accepted but not yet published: Tryon (in press) or (Tryon, in press).
 8. Unpublished material: G. Crow (submitted); G. Crow (unpubl. data); G. Crow (pers. obs.); or (G. Crow, pers. comm.); unless otherwise listed or cited in the manuscript or a nationally known authority, professional affiliation should also be given.
- References to companies manufacturing products used in a study should not appear in the Literature Cited. Rather, the company name and location should be given in parentheses within the text [e.g., SYSTAT (SPSS, Chicago, Illinois)].
- Authors of scientific names should be cited for all taxa at the rank of genus and below either at their first usage in the text or in a table or appendix (e.g., in a flora or table of voucher specimens). It should be indicated which taxonomic treatment, revision, or flora nomenclature follows. Use standard abbreviations for author’s names found in <http://www.rbgkew.org.uk/data/authors.html> or *Authors of Plant Names* by R. K. Brummitt and C. E. Powell.

- Names of publications cited in the text should be in italics.
- Avoid abbreviations in the text unless indicating measurement, then use a period unless abbreviating a metric term. Other abbreviations should be defined when first used [e.g., Scanning Electron Microscopy (SEM)]. Herbarium acronyms should follow <http://www.nybg.org/bsci/ih/> or *Index Herbariorum*, most recent edition.
- Numbers one through nine should be written out in the text unless a measurement or part of a taxonomic description. No comma is used with 4-digit numbers. A number should always precede a decimal point (e.g., 0.15).
- Back-to-back parentheses should be avoided by using a semi-colon. Parentheses within parentheses should be avoided by using outer brackets.

Taxonomic Treatments

- Use boldface Roman type for new names and new combinations, followed by “*sp. nov.*”, “*comb. nov.*”, etc.
- For nomenclatural history (i.e., synonymy and typification) use one paragraph per basionym [e.g., *Binomial* author, literature citation. TYPE: collection information from least-to-most-specific, *collector(s) collection number* (Holotype: herbarium acronym; Isotypes: herbarium acronym(s).)].
- Exclamation points are used for type specimens examined, and types not seen are indicated as such (e.g., GH!, MO not seen).
- Lectotype designations are included together with an indication of where they were designated, what year, and by whom. This reference is listed in the Literature Cited. If the author of the paper is making

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- Standard abbreviations for author’s names should be used according to <http://www.rbgekew.org.uk/data/authors.html> or *Authors of Plant Names* by R. K. Brummitt and C. E. Powell.
- When dates are given as part of collection information, 3-letter abbreviations with no period are used for months.
- Use <http://www.nybg.org/bsci/ih/> or *Index Herbariorum*, most recent edition, for herbarium acronyms.
- Designation of a new taxon should include a brief Latin diagnosis, rather than a full Latin description, which sets forth succinctly how the new taxon differs from its congeners.
- A full description, in English, should follow. This should be parallel with other descriptions at the same rank in the paper, and should not repeat information given in any description of the inclusive taxon (i.e., species descriptions should not repeat information characteristic of the genus, if also described in the paper). All measurements are metric. Hyphens are used for parenthetical extremes. A multiplication symbol is used where appropriate, rather than the letter x.
- Following the description, information should be given on distribution, ecology, uses, and nomenclature and typification, where appropriate. The discussions should be parallel within a given rank. For newly described taxa, this discus-

sion should explain clearly how the new taxon differs in these characteristics from closely related taxa.

- A high-quality line drawing or photograph of the type specimen, illustrating the diagnostic features, should be included for new taxa.
- Specimen citation should be selected critically, especially for common species of broad distribution. A title such as “Specimens examined” or “Representative specimens examined” should be indented, in upper and lower case, followed by a period. Each country begins a new paragraph. The format of information is as follows: COUNTRY. Major political division such as state: smaller political division such as county, detailed location, date (e.g., 26 Sep 1950), *collector(s) last name(s) collection number or s.n.* (herbarium acronym).

Keys

- Keys are dichotomous and indented.
- Leads of each couplet are parallel.
- Information in the key is consistent with that in descriptions, text, tables, and figures.

Data and Voucher Specimens

- Voucher specimens must be cited in a table or appendix to document sources of morphological or molecular data. Format for citation is the same as that for “specimens examined” as part of taxonomic treatments.
- All sequences used as data must be deposited in one of the international nucleotide sequence databases, and sequence database accession numbers included in the paper (GenBank: gsdb@gsdb.ncgr.org).
- All data matrices used in cladistic analyses should be deposited in TreeBASE (<http://www.herbaria.harvard.edu/treebase>).

Floras

- Long lists of taxa are best treated as an Appendix, so that the readability of the text is not compromised, and so that the list may be used independently by readers.
- A short introductory paragraph explaining terms or abbreviations used in the list of taxa should follow the Appendix title (see Searcy and Hickler 1999, *Rhodora* 101: 356).
- Three levels of headings are possible in lists of taxa: first-level is centered, all capitals, bold (e.g., **ANGIOSPERMAE** or **MAGNOLIOPSIDA**); second-level is centered, all capitals, not bold (e.g., **MONOCOTYLEDONEAE** or **LILIIDAE**); third level is flush left, all capitals, bold (e.g., **ACORACEAE**; this level will be converted to small caps by the printer).
- Taxa should be listed alphabetically within each hierarchical category (e.g., species alphabetically within the genus; genera alphabetically within family).
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- An indication of ecological preference, distribution within the area studied, and abundance should be included, where appropriate.
- Voucher specimens should be listed (collector, collection number, and herbarium acronym; information common to all or most vouchers can be stated in an introductory paragraph).

Acknowledgments

- Acknowledgments should be brief.
- Information on granting agencies, herbaria from which loans were obtained, artists, and colleagues or advisors who have critically re-

viewed the manuscript should be included.

- The word “Acknowledgments” should be indented, in all capital letters, followed by a period, and should appear on the first line of the acknowledgments.

Literature Cited

- The Literature Cited contains all references cited in the text and vice versa.
- The alternative of a general “References” section requires prior approval by the Editor.
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- Cite references in alphabetical order by first author’s last name. Entries by a single author should precede multi-authored works with the same first author, regardless of date.
- List works by the same author chronologically, beginning with earliest date of publication.
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Tables

- Each table should be cited in the text in numerical order.
- Each table starts on a separate sheet and is fully double-spaced. If necessary, table may be continued on a second page. Do not single-space or use a smaller font in order to fit a large table onto a single page.
- Landscape (or broadside) formatting should be avoided, if possible.
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top of the table. Do not submit a separate sheet of table captions.

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- Do not use vertical lines in tables.

Figure Legends

- Figure legends should appear together on a page separate from the illustrations. Do not use a separate page for each figure legend.
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- Illustrations must be either black and white half-tones (photographs), drawings, or graphs. Color photographs must be paid for by the author(s), and require prior approval of the Editor.
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of this, italicized words must be printed in italics, and all names and terms must be consistent with those used in the text. This includes any capitalization as well as spelling.

- All illustrations must have at least a 1-inch margin on all sides.
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- Write author(s) name(s) and figure number(s) on the back of each camera-ready figure or plate.

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- The Notes and New England Notes sections are available for short contributions that augment a recent publication or contribute to our knowledge of the flora. While these papers do not typically contribute new experimental data, they must have the scientific merit of longer papers, and must include references to pertinent literature, a discussion of scientific significance, and vouchered collections, where appropriate.
- Submissions in this category should not include an abstract, key words, or sections such as Materials and Methods or Results.
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- In general, guidelines for longer articles should be followed.

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- It is the author's responsibility to verify all information included in the manuscript.
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should have been read critically by all coauthors.

- The manuscript should be checked against these instructions. Manuscripts not properly prepared may be returned for revision prior to review.
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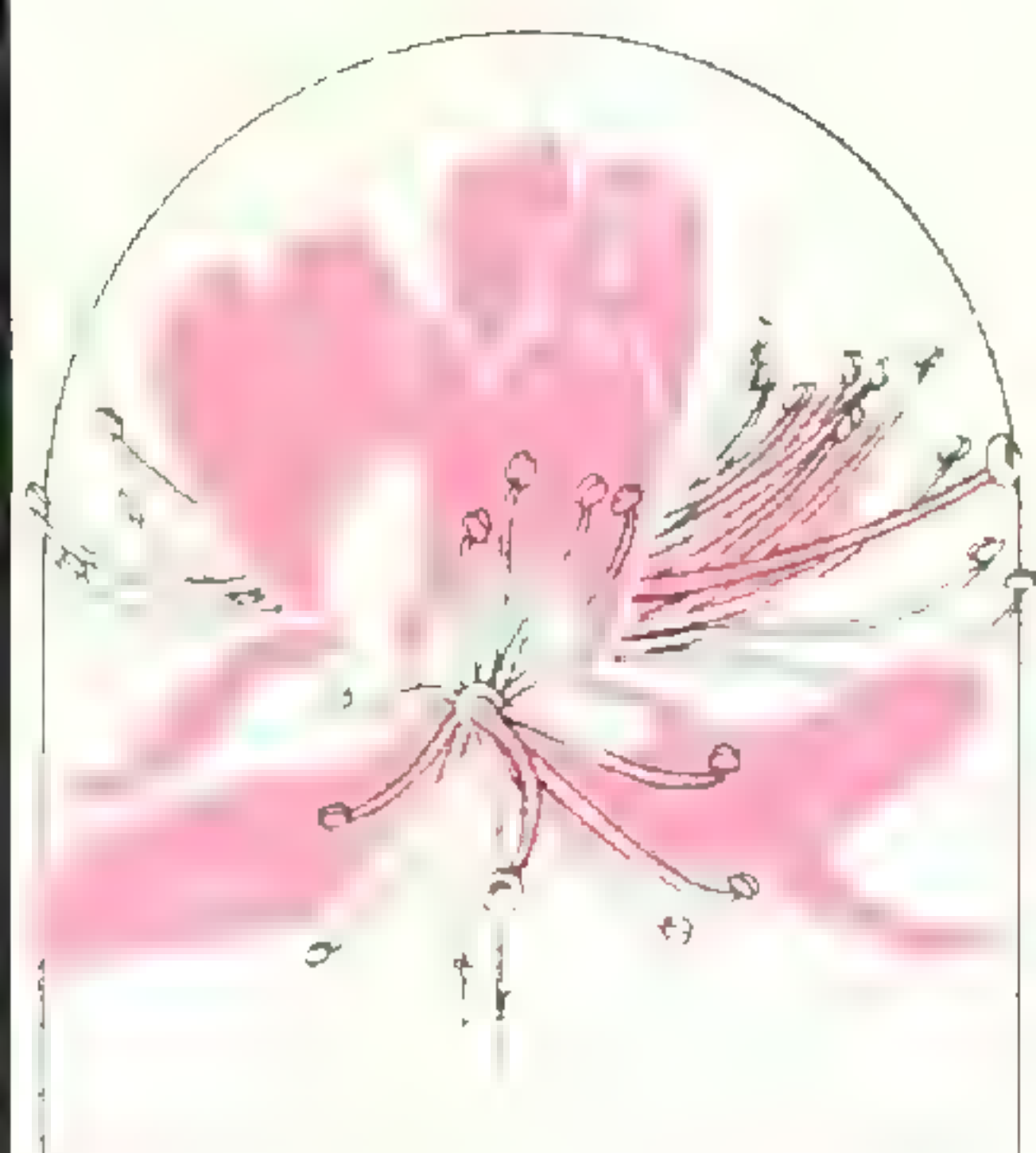
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PHYLOGENETICS OF *BUCKLEYA* (SANTALACEAE)
BASED ON ITS SEQUENCES OF NUCLEAR
RIBOSOMAL DNA

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ABSTRACT. *Buckleya* (Santalaceae) is a hemi-parasitic, shrubby genus with two species in China, one in Japan, and one in the southeastern United States. Phylogenetic relationships among these species are controversial and have not been tested using molecular data. In this study we used sequences of the internal transcribed spacer region of nuclear ribosomal DNA to test previous phylogenetic hypotheses. Two sister species pairs are well supported: *B. distichophylla* plus *B. graebneriana*, and *B. lanceolata* plus *B. henryi*. Sequence differences and morphological characters support the recognition of *B. lanceolata* and *B. henryi*. Sequence divergence between *B. distichophylla* and *B. graebneriana* is twice as high as that between *B. lanceolata* and *B. henryi*. These results are most consistent with the treatment proposed by Carvell and Eshbaugh. Biogeographically, one of the Chinese species (*B. graebneriana*) is most closely related to the eastern North American species (*B. distichophylla*), while the other Chinese species (*B. henryi*) is allied with the Japanese species (*B. lanceolata*). Maximum likelihood analyses do not reject clock-like evolution of nrDNA ITS spacers in *Buckleya*, and divergence times may date to the Late Miocene and Pliocene.

Key Words: biogeography, *Buckleya*, Santalaceae, ITS, phylogeny, molecular clock

The Santalaceae comprises more than 30 genera, most of which are restricted to either the Old or New Worlds (Kuijt 1969). *Buckleya* Torr. (piratebush), however, is one of a few exceptions having a disjunct distribution in both the Old and New Worlds. Of the four species, one, *B. distichophylla* (Nutt.) Torr., is rare and local in the southern Blue Ridge Mountains of the southeastern United States (Musselman and Mann 1978), while the others are in eastern Asia, with one species widespread in Japan and two

species locally common in east central China. In Japan, *B. lanceolata* (Siebold & Zucc.) Miq. is endemic to Honshu, Shikoku (Carvell and Eshbaugh 1982), and perhaps also to Kyushu (Hara 1959; Horikawa 1976). Both *B. henryi* Diels and *B. graebneriana* Diels are endemic to China. The former is more widely distributed (Gansu, Shaanxi, Anhui, and Zhejiang) than the latter (Gansu, Shaanxi, and Henan).

Species of *Buckleya* form haustoria on a variety of hosts, including *Taxus*, *Pinus*, *Chamaecyparis*, *Abies*, *Cryptomeria*, and some hardwoods, both in nature and in culture (Kusano 1902; Musselman and Mann 1978; Piehl 1965). *Buckleya* is of minor economic value; the fruits are rich in starch and have long been pickled and sold as a condiment in both China and Japan. The young leaves and the bark are reported to be poisonous and irritating to the skin (Howard 1984). *Buckleya* can be distinguished easily from other genera of the Santalaceae by its distichous leaf arrangement and elliptic or rounded fruits with apical foliaceous bracts. There is little doubt that *Buckleya* is monophyletic on the basis of these distinctive morphological traits, and this is also supported by a broader phylogenetic analysis based on nrDNA internal transcribed spacer (ITS) sequences (Li and Nickrent, unpubl. data).

Buckleya was discovered by Thomas Nuttall in 1816 (Nuttall 1818), and placed in the genus *Borya* Willd. (Oleaceae). *Borya* was later replaced by the conserved name *Forestiera* Poir. (Oleaceae). Torrey (1843), using material collected by S. B. Buckley, correctly noted its affinity to the Santalaceae. By the beginning of the twentieth century all four species had been described (Diels 1900; Miquel 1870).

Pilger (1935) placed the four species in two sections on the basis of bract persistence before fruit maturity: sect. *Eubuckleya*, characterized by deciduous bracts and including only the North American *Buckleya distichophylla*; and sect. *Quadriala*, defined by enlarged and persistent bracts and containing all three Asiatic species. Carvell and Eshbaugh (1982, p. 33), however, disagreed with Pilger's taxonomy and proposed instead that *B. henryi* and *B. lanceolata* are closely related and that "*Buckleya distichophylla* and *B. graebneriana* differ significantly from this group and do not appear to show a close affinity to each other."

In this study we tested both Pilger's and Carvell and Eshbaugh's hypotheses on interspecific relationships using sequences

Table 1. Specimens used in this analysis (S = staminate, P = pistillate). Vouchers are deposited in A.

Sample	Species	Collector	Locality	Note	GenBank#
1	<i>Buckleya henryi</i>	<i>Boufford et al.</i> 26105	Henan, China	S	AF291906
2	<i>B. henryi</i>	<i>Boufford et al.</i> 26290	Henan, China	P	AF291900
3	<i>B. henryi</i>	<i>Boufford et al.</i> 26201	Henan, China	P	AF291907
4	<i>B. lanceolata</i>	<i>Yonekura et al.</i> 95537	Fukushima, Japan	S	AF291904
5	<i>B. lanceolata</i>	<i>Boufford et al.</i> 25361B	Miyage, Japan	P	AF291903
6	<i>B. lanceolata</i>	<i>R. Nishimura</i> 909	Honshu, Japan	P	AF291902
7	<i>B. graebneriana</i>	<i>Boufford et al.</i> 26521	Henan, China	P	AF291899
8	<i>B. graebneriana</i>	<i>Boufford et al.</i> 26520	Henan, China	P	AF291905
9	<i>B. distichophylla</i>	<i>Boufford et al.</i> 5/4/98	Tennessee, U.S.A.	P	AF291901
10	<i>Thesium impeditum</i>	<i>Kim Steiner, s.n.</i>	Natal, South Africa		AF291908

of the **ITS** region of nuclear ribosomal DNA. This region has been widely used for resolving relationships at lower taxonomic levels (Baldwin et al. 1995; Li and Donoghue 1999; Li et al. 1997; Liston et al. 1999). Fossils of *Buckleya* are unknown, but we have used sequence information to provide a range of estimated times of divergence.

MATERIALS AND METHODS

Plant material. Nine individuals were sampled from recently collected herbarium specimens of the four species of *Buckleya*: *B. distichophylla* (one pistillate individual), *B. graebneriana* (two pistillate individuals), *B. henryi* (one staminate and two pistillate individuals), and *B. lanceolata* (one staminate and two pistillate individuals). *Thesium impeditum* Hill (Santalaceae) was included in the analysis for rooting purposes; DNA of this species was kindly provided by Dan Nickrent of Southern Illinois State University (Table 1).

Molecular techniques. About 20 mg of dried leaf material were removed from each of the specimens. The DNA was ex-

tracted using the Qiagen Plant DNAeasy Kit (Qiagen Inc., Santa Clarita, CA), following the manufacturer's instructions. The polymerase chain reaction (PCR) was performed using the primer pairs ITS4 and ITS5 of White et al. (1990) in a Perkin Elmer thermocycler. Each 25 μ l reaction included 50–100 ng genomic DNA, 2.5 μ l of 10 $\times$ PCR buffer (Gibcol BRL, Grand Island, NY), 0.8 μ l of 50 μ M MgCl₂, 4 μ l of dNTP (2.5 μ M), 1 μ l of 10 μ M primers, 1–1.5 units of Taq polymerase (Gibcol BRL), and an appropriate amount of distilled water. The PCR thermocycler program consisted of 35 cycles of denaturation at 94°C (30 sec.), annealing at 55°C (60 sec.), and extension at 72°C (115 sec.), followed by a 7 min. extension at 72°C. The PCR products, identified by comparison with the low mass DNA size marker (Gibcol BRL), were purified in a 1% agarose gel, and were then extracted using a Qiagen gel extraction kit (Qiagen Inc., Santa Clarita, CA). Purified PCR product was used directly as a template for sequencing reactions using a cycle sequencing kit (Applied Biosystems, Foster City, CA) and primers ITS4 and ITS5 of White et al. (1990) and ITS3B (Baum et al. 1998). The sequences were obtained using an ABI 377 Automated Sequencer, analyzed using Sequencher 3.0 (Gene Codes Corp., Inc., Ann Arbor, MI), and then aligned manually.

Phylogenetic analyses. Parsimony analyses were conducted using the exhaustive search algorithm in PAUP* (version 4.0b3, Swofford 2000). All characters were equally weighted and character state changes were unordered. Gaps were treated as missing. The sister group of *Buckleya* is unclear, since intergeneric relationships in the Santalaceae have not been analysed in detail. However, in a phylogenetic analysis of Santalales, which included 12 genera of Santalaceae *s.l.*, *Thesium* appeared to be most closely related to *Buckleya* (Nickrent et al. 1998). *Thesium impeditum* was therefore included for rooting. Decay analysis (Bremer 1988; Donoghue et al. 1992) and five hundred replicate bootstrap analyses (Felsenstein 1985) were conducted to assess relative support for clades.

Estimate of divergence time. To determine whether the ITS region in *Buckleya* evolved in a clocklike fashion or not, the maximum likelihood ratio (MLR) test was conducted using PAUP* 4.0b3 following Baum et al. (1998). One individual from

Table 2. ITS sequence divergence in *Buckleya* (Kimura 2-parameter distance $\times$ 100, calculated using PAUP*).

Species	1	2	3	4	5	6	7	8	9	10
1. <i>B. henryi</i>	–									
2. <i>B. henryi</i>	0.0									
3. <i>B. henryi</i>	0.1	0.0	–							
4. <i>B. lanceolata</i>	3.5	3.7	3.7							
5. <i>B. lanceolata</i>	3.5	3.7	3.7	0.0	–					
6. <i>B. lanceolata</i>	3.5	3.7	3.7	0.0	0.0	–				
7. <i>B. graebneriana</i>	13.3	13.3	13.3	13.7	13.7	13.7	–			
8. <i>B. graebneriana</i>	12.4	12.5	12.5	12.9	12.9	12.9	0.6	–		
9. <i>B. distichophylla</i>	13.9	13.9	13.9	13.5	13.5	13.5	7.1	6.5		
10. <i>Thesium impeditum</i>	28.8	28.8	28.8	30.9	30.9	30.9	32.3	31.6	31.2	–

each species was used in the MLR test and several models were applied to the reduced data set, including F81, F84, and HKY (Baum et al. 1998). There have been several estimated evolutionary rates for the ITS region. We used both the lowest (3.2×10^{-10} base substitution per site per year; Suh et al. 1993) and highest (7.8×10^{-9} base substitution per site per year; Sang et al. 1995) of these rates.

RESULTS

Sequences of all accessions varied in length between 668 and 732 base pairs (bp), and within *Buckleya* from 719 to 732 bp. Alignment of the ten sequences produced a data matrix of 755 characters, requiring 120 gaps, 20 of which were parsimony informative. There were 233 variable sites, of which 100 were parsimony informative. There was little sequence variation ($< 0.6\%$) within each species, while sequence divergence between species ranged from 3.5 to 13.9% (Table 2). Twelve informative indels, ranging from one to six bases, were found in the ITS sequences of *Buckleya* (Table 3). Two indels marked *B. graebneriana* (6 and 8 in Table 3), three marked *B. distichophylla* (3, 7, and 9), and six marked *B. lanceolata* and *B. henryi* (1–2, 4–5, and 10–12). GenBank accession numbers are listed in Table 1 and the matrix of aligned sequences is available from TreeBASE (<http://phylogeny.harvard.edu/treebase>; accession # M753).

A parsimony analysis generated a single shortest tree of 276 steps (Figure 1, CI = 0.96, RI = 0.95). Individuals of each species are united with strong bootstrap and decay support. Also well

Table 3. Informative indels in the ITS sequences of *Buckleya*.

Indel	1	2	3	4	5	6	7	8	9	10	11	12
Site	5	100	128	136	176	212	316	488	494	541	544	591
				-141		-213	-317	-489	-497		-545	
<i>B. distichophylla</i>												
			-	GAT--G	-	--	--	GT	----	.	--	-
<i>B. graebneriana</i>												
	-	-	-/T	GACGAC	-	TG	GA	--	--CA	-	--	-
<i>B. henryi</i>												
	G	T	G	-----	A	--	CG	GT	AAGC	G	TG	A
<i>B. lanceolata</i>												
	G	T	G	-----	A	--	CG	GT	-ACA	G	TG	A

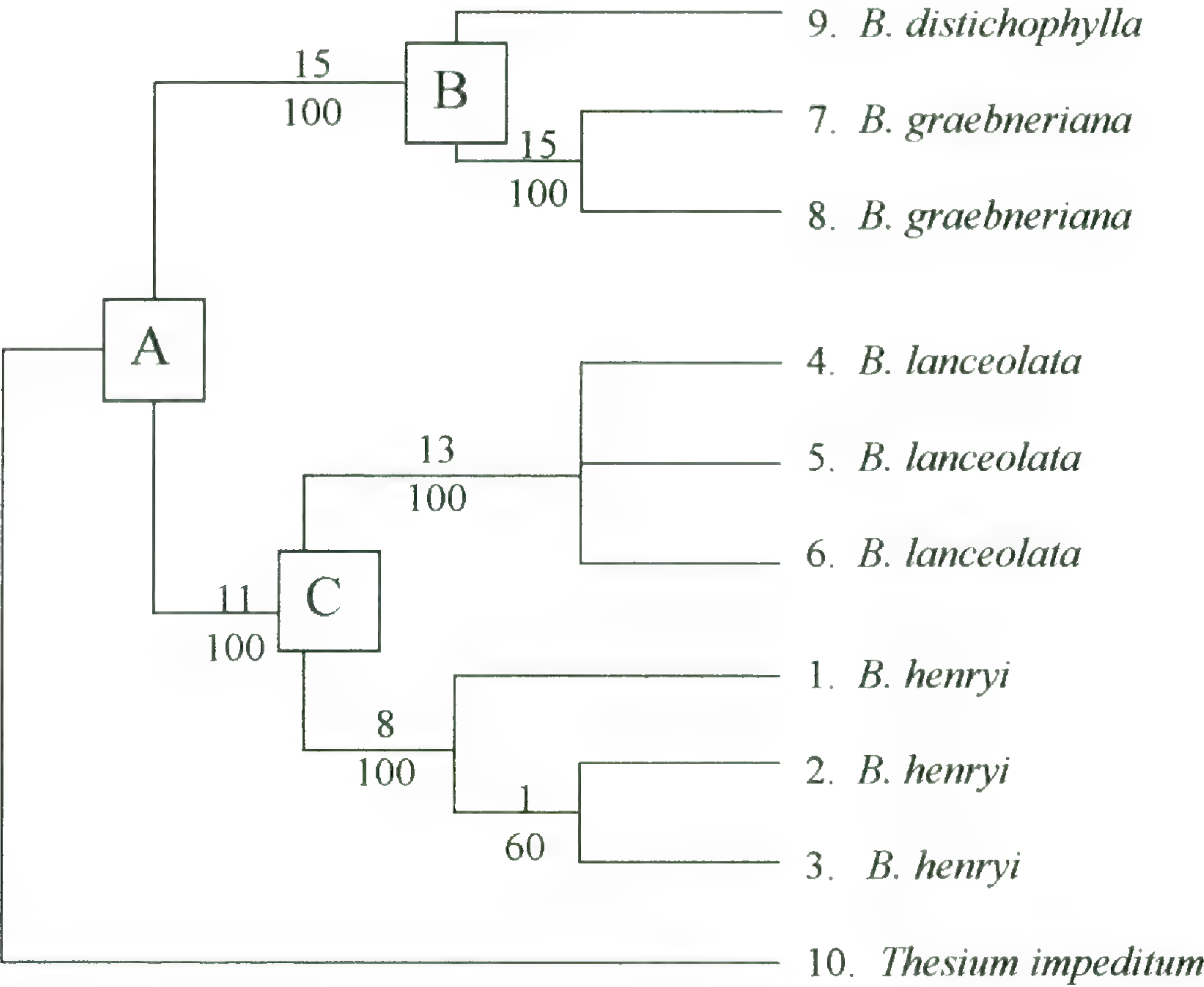


Figure 1. The single tree of 276 steps for *Buckleya* (CI = 0.96, RI = 0.95). Estimated times of divergence are as follows: A, 8.5 MYA, B, 5 MYA, and C, 2.4 MYA. Numbers above and below branches are decay values and bootstrap percentages, respectively.

supported are the species pairs of *Buckleya distichophylla*–*B. graebneriana* and *B. lanceolata*–*B. henryi*.

The maximum likelihood ratio test using different models did not reject the null hypothesis that the ITS region in *Buckleya* evolved in a clocklike fashion ($P > 0.05$). Using the rate of 3.2×10^{-10} base substitutions per site per year, the estimated time of divergence of the two species pairs, *B. distichophylla*–*B. graebneriana* and *B. lanceolata*–*B. henryi*, was 207 MYA. This seems unlikely as it predates the presumed radiation of angiosperms (Doyle 1998). Using the rate of 7.8×10^{-9} base substitution per site per year, the two species pairs, *B. distichophylla*–*B. graebneriana* and *B. lanceolata*–*B. henryi*, diverged from one another at around 8.5 MYA, and the estimated times of divergence between *B. distichophylla* and *B. graebneriana*, and between *B. lanceolata* and *B. henryi* were 5 and 2.4 MYA, respectively. These estimates seem more likely in view of the observation that rates of nucleotide substitution may be elevated in parasitic and hemi-parasitic plants (Nickrent et al. 1998).

DISCUSSION

ITS sequence divergence. Several studies have shown that the ITS region is not variable enough to resolve relationships among morphologically similar woody plants (e.g., *Hamamelis*, Li et al. 2000; Wen and Shi 1999; *Cercis*, Davis et al., unpubl. data). This does not appear to be the case for parasitic or hemi-parasitic plant groups, although the data are still limited. For example, Nickrent and Starr (1994) found that high substitution rates in ITS sequences of *Viscum* (Santalaceae) created difficulties in sequence alignment. In *Buckleya*, interspecific variation can be as high as about 14%, two to three times higher than in non-parasitic woody angiosperms (Baldwin et al. 1995; Wen and Shi 1999).

Phylogenetic relationships. Both Pilger (1935) and Carvell and Eshbaugh (1982) recognized four species in *Buckleya*, whereas Kiu and Lin (1988) treated *B. henryi* as a synonym of *B. lanceolata*. As pointed out by Carvell and Eshbaugh (1982), however, *B. henryi* is easily distinguished from *B. lanceolata*. In *B. henryi* the bracts are elliptic and twice as long as the fruit (vs. oblanceolate, and three times as long as the fruit in *B. lanceolata*);

the leaf tips are acuminate and are not markedly caudate (vs. lanceolate-acuminate and notably caudate in *B. lanceolata*); and the flowers are both terminal and axillary (vs. terminal, rarely axillary male inflorescences in *B. lanceolata*). Because *B. henryi* is restricted to China and *B. lanceolata* is endemic to Japan, the two species do not occur sympatrically, as reported by Kiu and Lin (1988). Our results show that there are few base substitutions within the same species ($< 0.6\%$ sequence divergence), but between different species sequence divergences range from 3.5 to 13.9%. The molecular evidence, which shows a 3.5–3.7% sequence divergence between *B. henryi* and *B. lanceolata*, provides further support for the recognition of the two species as distinct.

Pilger (1935) noted that the bracts and sepals of the Asiatic species of *Buckleya* remained closely attached to the fruit before fruit maturity, and as a result he recognized two sections: the North American *B. distichophylla* in section *Eubuckleya*, and all three Asiatic species in section *Quadriala*. Carvell and Eshbaugh (1982), however, noted that *B. distichophylla* and *B. graebneriana* share the attribute of non-striate ovaries, reflective of weaker vascular connections between the floral tube and the bracts (Smith and Smith 1943). Further, deciduous bracts occur not only in *B. distichophylla* but also in *B. graebneriana*, suggesting a close relationship of these two species. Additional characters supporting the close relationship of the two species pairs (*B. henryi*–*B. lanceolata* and *B. distichophylla*–*B. graebneriana*) include inflorescence position, and the coloration of the buds, branchlets, and scale tip of the leaves (Table 4). These observations led Carvell and Eshbaugh (1982) to reject Pilger's sectional classification of *Buckleya*. Nonetheless, they recognized the close relationship of *B. henryi* and *B. lanceolata*, as suggested by Pilger (1935).

In this study, the sequence divergence between *Buckleya distichophylla* and *B. graebneriana* is from 6.5–7.1%, which is much less than that between *B. distichophylla* and either *B. henryi* or *B. lanceolata* (13.5–13.9%). The two species pairs are also comparable in terms of number of base substitutions and indels supporting each pair. There are 30 base changes and 9 indels supporting *B. distichophylla*–*B. graebneriana*, and 38 and 8 for *B. henryi*–*B. lanceolata*. Thus, our results support Carvell and Eshbaugh's (1982) hypothesis on the interspecific relationships in *Buckleya*. It should be noted, however, that *B. henryi* and *B. distichophylla* are remarkably similar in overall aspect and ecolog-

Table 4. Morphological variation of species of *Buckleya* (Carvell and Eshbaugh 1982 and our observations).

Character	<i>B. distichophylla</i>	<i>B. graebneriana</i>	<i>B. lanceolata</i>	<i>B. henryi</i>
Habit	Shrub to 4 m tall, stems arching	Shrub to 2 m tall, stems erect	Shrub 2 m tall, stems erect	Shrub 2.5 m tall, stems arching
Trichomes	Unicellular, conical to papillate, sparse	Unicellular, soft needle-shaped, conical to papillate, dense	Multicellular, filiform, or unicellular, conical to papillate, dense	Unicellular, conical to papillate, sparse
Bark	Gray	Gray	Pale gray	Grayish brown
Bud color	Light tan	Light tan	Red-brown	Red-brown
Bud shape	Lanceoloid	Ovoid	Ovate	Ovoid
Upper leaves on branchlet	Lanceolate, apex often slightly curved, shortly attenuate	Elliptic to ovate, acuminate to acute, shortly attenuate	Lanceolate-acuminate, apex slightly curved, markedly caudate	Lanceolate, acuminate, tip slightly curved, attenuate to shortly attenuate
Lower leaves on branchlet	Elliptic, acute, shortly attenuate	Obovate, cuspidate, shortly attenuate	Elliptic, acuminate, caudate, shortly attenuate	Elliptic, acute, shortly attenuate, puberulent above
Leaf scale tip	Whitish-yellow	Whitish-yellow	Reddish-brown	Reddish-brown
Flowers	Male and female terminal	Male and female terminal	Male terminal and rarely axillary; female terminal	Male terminal and axillary; female terminal
Bract	Narrowly elliptic to lanceolate, deciduous, as long as or slightly longer than fruit	Lanceolate, deciduous, as long as or slightly longer than fruit	Oblanceolate to narrowly elliptic, persistent, three times as long as fruit	Narrowly elliptic, persistent, two times as long as fruit
Fruit	Not striate, ellipsoid to ovoid, puberulent	Not striate, fusiform, glabrous	8-striate, ellipsoid to obovoid, glabrous to densely puberulent	8-striate, ellipsoid to obovoid, glabrous to densely puberulent

ical preference. Both grow on moist slopes along streams, both attain roughly the same height, and both exhibit the same overall gestalt as they arch gracefully over rocky boulders amongst the surrounding vegetation. In contrast, *B. graebneriana* is a low, stiffly erect, densely colonial shrub adapted to more xeric conditions along the crests of ridges and on well drained slopes. *Buckleya lanceolata* appears more similar to *B. distichophylla* and *B. henryi* in general habit and habitat preference; we presume this is a retained ancestral condition.

Biogeography. Floristic affinities between eastern North America and eastern Asia have long been known, as exemplified by disjunct distributions of species in many genera (Boufford and Spongberg 1984; Hong 1993; Wen 1999). A general phylogenetic pattern has recently been identified based on a comparison of molecular phylogenies of seven disjunct plant genera (Wen 1999; Xiang et al. 1998, 2000). In these groups it appears that the eastern and western North American species are more closely related to one another than they are to Asian species. Several other recent phylogenetic studies indicate that the Xiang et al. (1998) pattern is part of several broader patterns when areas of endemism within Asia are taken into account. For example, the Japanese and North American species of *Hamamelis* are more closely related to one another than they are to the Chinese species (Li et al. 2000; Wen and Shi 1999). This is also true for species of *Viburnum* section *Pseudotinus* (Adoxaceae; Donoghue and Li, unpubl. data), and is consistent with an analysis of *Weigela* and *Diervilla* (Caprifoliaceae; Kim and Kim 1999). In contrast, in *Triosteum* (Caprifoliaceae) the Chinese and North American species are more closely related to one another than they are to the Japanese species (Gould and Donoghue 2000).

The results for *Buckleya* reveal yet another pattern, which is perhaps most similar to that seen in *Triosteum*. Here the single North American species, *B. distichophylla*, is linked with one of the Chinese species, *B. graebneriana*, while the Japanese species, *B. lanceolata*, is most closely related to the second Chinese species, *B. henryi*. The difference between the *Buckleya* and the *Triosteum* patterns is that in *Buckleya* the Japanese species, *B. lanceolata*, and the Chinese species, *B. henryi*, are differentiated both on the basis of morphological and ITS data, and generally, as here, are recognized as separate species. In contrast, popula-

tions of *T. sinuatum* Maxim. from Japan and from northeastern China do not appear to be differentiated and have been treated as conspecific.

The biogeographic history of *Buckleya* is difficult to understand without fossil evidence. We note, however, that estimated divergence times, based on several ITS nucleotide substitution rates, are in the late Miocene and Pliocene, when migration between Europe and eastern North America was difficult via the North Atlantic (Tiffney 1985), though perhaps still possible for fleshy-fruited, potentially bird-dispersed plants such as *Buckleya*. Exchange between the Old and New World was possible more recently across Beringia. Phylogenetic analyses of many additional disjunct taxa are needed in order to uncover general patterns that may implicate particular pathways and vicarious events.

KEY TO SPECIES

1. Scale tip of leaf whitish-yellow; fruits without distinct vascular strands, without longitudinal striations on ovary; bracts deciduous (2)
1. Scale tip of leaf reddish-brown; fruits with vascular strands evident as longitudinal striations on ovary; bracts persistent (3)
2. Lower leaves elliptic, acute; upper leaves lanceolate with slightly curved apex; trichomes in inflorescence conical to papillate, ca. 0.1 mm long; plants solitary, stems arching *B. distichophylla*
2. Lower leaves obovate, cuspidate; upper leaves elliptic to ovate, acuminate; trichomes in inflorescence elongate, ca. 0.5 mm long; plants colonial, stems erect *B. graebneriana*
3. Bracts elliptic, 2 times as long as fruit; leaves not markedly caudate; trichomes sparse *B. henryi*
3. Bracts oblanceolate, 3 times as long as fruit, leaves markedly caudate, trichomes dense *B. lanceolata*

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INSIGHTS INTO THE SPECIES DELINEATION AND
POPULATION STRUCTURE OF *SOLIDAGO SHORTII*
(ASTERACEAE) THROUGH MORPHOMETRIC ANALYSIS

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ABSTRACT. Short's goldenrod, *Solidago shortii* (Asteraceae), is extant from a single locality in Blue Licks, Kentucky. Field studies demonstrated that this endemic is a morphologically variable taxon, inspiring two questions. First, is the taxon known as *S. shortii* from Blue Licks the same species as originally described by Torrey and Gray from an extirpated population at the Falls of the Ohio River, Kentucky? Second, what is the extent of the morphological variation within and among populations of Short's goldenrod at Blue Licks? These questions were addressed through Principal Components Analysis (PCA), Discriminant Function Analysis (DFA), and standard whole-plant herbarium specimen comparisons. Whole-plant comparisons with other members of *Solidago* subsection *Triplinervae* revealed diagnostic characters suitable for the delineation of *S. shortii*. All specimens of *S. shortii* from both the Blue Licks and Falls of the Ohio localities shared diagnostic character states. For morphometric purposes, specimens representing two sympatric goldenrod species (*S. ulmifolia* and *S. nemoralis*) and one close phylogenetic relative (*S. canadensis* var. *scabra*) were sampled from the same locality as *S. shortii*. Vegetative and floral characters were analyzed for all four taxa. Specimens of *S. shortii* from the Blue Licks vicinity formed a continuous cluster in PCA with specimens from the Falls of the Ohio, a cluster which was distinct from those formed by the other three species. In DFA, the Falls of the Ohio specimens were imbedded in the cluster formed by the Blue Licks specimens. Thus, the taxon at Blue Licks is indeed *S. shortii*, as established by morphometric analysis and whole-plant comparisons. In terms of interspecific variation, *S. shortii* at Blue Licks exhibited a similar or greater range of variation than either of the two more common *Solidago* taxa found at Blue Licks, *S. canadensis* var. *scabra* and *S. nemoralis*. The range of

morphological variation exhibited by *S. ulmifolia* was slightly greater than that of *S. shortii*. These data also indicate a greater variability within and among Blue Licks populations of *S. shortii* than otherwise might be expected for a species of highly restricted distribution, and have major implications regarding management policies.

Key Words: intraspecific variation, morphometrics, species boundaries, *Solidago*, endangered species

There are 295 vascular plant species native to Kentucky (approximately 9.8% of the native flora) that are considered in danger of extinction (Endangered, Threatened, and Special Concern Plants and Animals of Kentucky, Kentucky Nature Preserves Commission, October 1992). One of the more unique species is Short's goldenrod, *Solidago shortii* Torr. & A. Gray, a member of the sunflower family (Asteraceae) and an entry on the Federal endangered species list [Federal Register Vol. 50(172): 36085–36089, 5 Sep 1985]. This species was first described by John Torrey and Asa Gray (1842) from a collection made by Dr. C. W. Short of Louisville from the Falls of the Ohio River in Jefferson County, Kentucky (Braun 1941). This original population was known to occur on Rock Island at the Falls of the Ohio River (Cronquist 1980), but has been extirpated by impoundment of the Ohio River (Evans 1987). The only known remaining populations of this species are from sites in and around Blue Licks Battlefield State Park, at the junction of Robertson, Nicholas, and Fleming Counties in north-central Kentucky (Figure 1A).

Solidago shortii occurs primarily in open, glade-like areas, often along the remnants of ancient buffalo (American bison) traces. The plants prefer open, sunny areas and do not compete well with other flowering plant species (Buchele et al. 1989). Invasion by non-native species, shading produced by woody taxa, and construction practices are among the major threats to the remaining plants. Recent surveys of the remaining sites identified 13 scattered populations of this species over an area of 12.2 km² (Buchele et al. 1989; Evans 1987; Figure 1A). It should be noted that population #13 is now extirpated, and population #6 has been reduced from a previous estimate of 2100 stems (Buchele et al. 1989) to less than 25 stems through intentional destruction by a resident landowner.

Prior investigations have focused on phenology and analysis

of life history. An exhaustive examination of autecological parameters included edaphic factors, light intensity, water relations, interspecific competition, and an overview of pollination ecology (Buchele et al. 1989, 1991, 1992a, 1992b). A subsequent series of studies focused on seed and seedling ecology, with evaluations of germination requirements, persistence of seeds in the seed soil bank, and effects of interspecific competition on seedlings (Walck et al. 1997a, 1997b, 1997c, 1997d, 1997e, 1998). Some general trends have emerged (e.g., the deleterious effect of interspecific competition on *Solidago shortii*). However, as is the case with many highly endemic species, a precise elucidation of the mechanism(s) responsible for the narrow endemism of *S. shortii* is not available (Buchele et al. 1992b; Walck et al. 1997a).

In the course of our field investigations into the population biology of *Solidago shortii*, we encountered a rather remarkable range of intra- and interpopulational morphological variation. Such variation had not been previously documented in the literature, and was not noted in several reports produced for state and federal agencies. In addition, we encountered some specimens of *S. shortii* that appeared to morphologically grade toward other *Solidago* congeners, initially creating considerable confusion and calling into question the exact nature of this species' delineation.

These observations brought two questions to mind. First, do the plants currently classified as Short's goldenrod at Blue Licks (BL) belong to that taxon as defined by the plants from the Falls of the Ohio (FO) type locality? Second, if the Blue Licks populations are indeed *Solidago shortii*, what level of intra- and interpopulational morphological variation exists in this highly restricted endemic, and how does this level of variability compare to congeners from the same geographic area?

We utilized morphometric analysis at both the inter- and intra-specific levels combined with whole-plant comparisons to address these questions. We compared herbarium specimens of *Solidago shortii* (BL and FO populations) with specimens of other members of the subsection *Triplinervae* (Torr. & A. Gray) A. Gray to obtain the macrocharacters most useful in defining *S. shortii*. To test the multivariate reality of *S. shortii* (as defined by whole-plant comparisons) we then compared the unit we believed to be *S. shortii* to one member of subsection *Triplinervae* [*S. canadensis* L. var. *scabra* (Willd.) Torr. & A. Gray] and to the two additional sympatric goldenrod species (*S. ulmifolia* Muhl. and *S.*

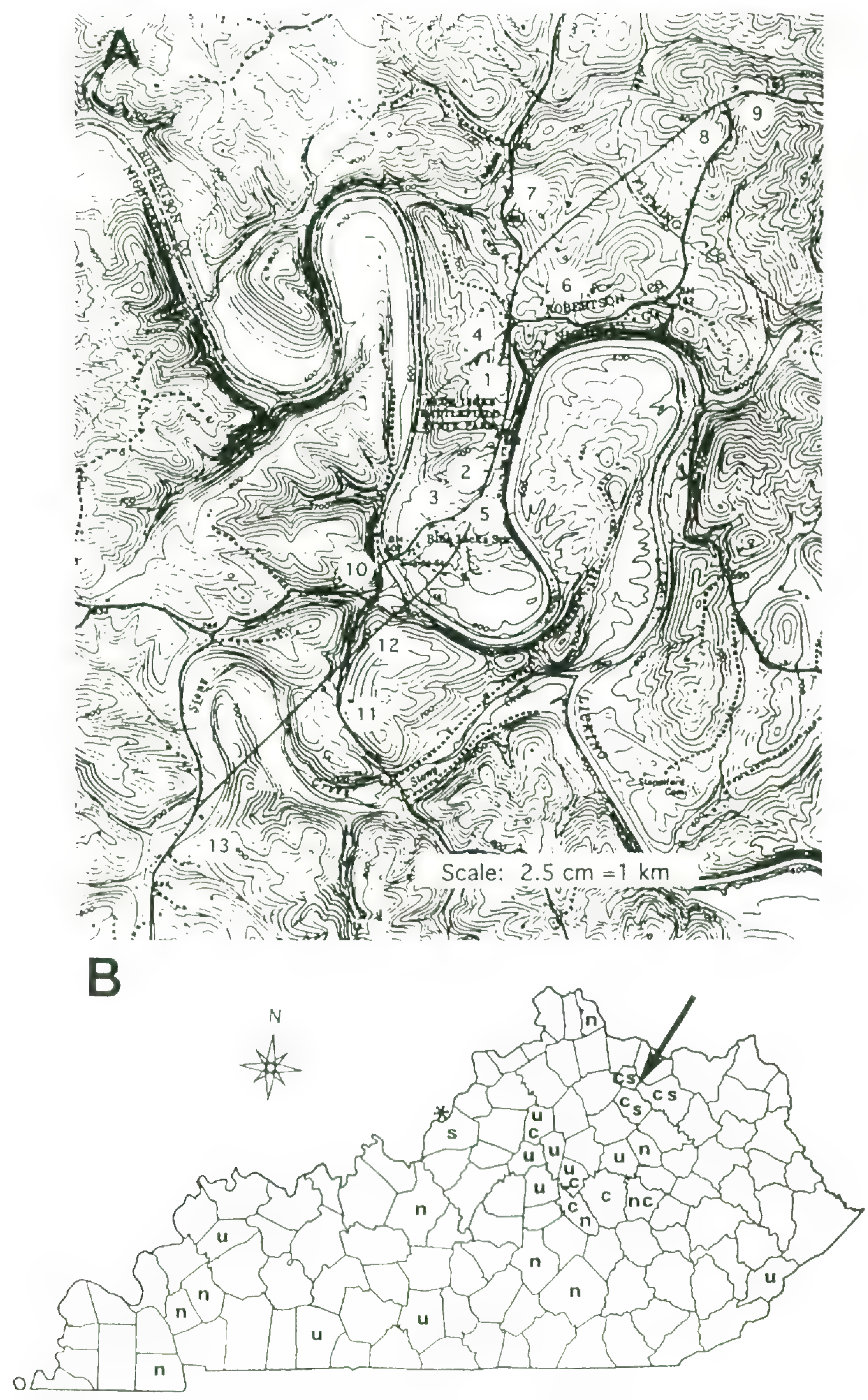


Figure 1. A. Map of the locality and known populations (1–12) of *Solidago shortii*, at the junction of Robertson, Fleming, and Nicholas counties in northern Kentucky. Populations #1, 7, 8, 9, 11, and 12 were sampled as described for morphometric analysis. The distribution map and numbering system is from Evans (1987). B. County map of Kentucky, showing the

nemoralis Aiton) using Principal Components Analysis (PCA) and Discriminate Function Analysis (DFA). In order to determine the range (quantitative limits) and distribution (intra- vs. inter-population) of the variation, we undertook a second morphometric analysis of sampled individuals from different populations of *S. shortii* at BL, treating each population as a separate entity and determining the extent of the morphological variation relative to other *S. shortii* populations.

MATERIALS AND METHODS

Whole-plant comparisons. Eighty herbarium specimens annotated as *Solidago shortii* were examined, including 21 specimens from the FO type locality. These were compared to specimens of the five members of the subsection *Triplinervae* present in the eastern United States (*S. canadensis*, *S. gigantea* Aiton, *S. rupestris* Raf., *S. leavenworthii* Torr. & A. Gray, and *S. tortifolia* Elliott) and to the two remaining *Solidago* species present at Blue Licks (*S. ulmifolia* and *S. nemoralis*). Characters useful in whole-plant diagnoses of species membership were noted.

Morphometric analysis. An initial herbarium study of 44 specimens representing the four taxa (*Solidago shortii*, *S. nemoralis*, *S. canadensis* var. *scabra*, and *S. ulmifolia*) was conducted to define those character states that would be most useful for morphometric comparisons (county localities indicated in Figure 1B). Nineteen characters (Table 1; Figure 2) were considered. Fourteen *S. shortii* specimens were measured, including seven collected from the type locality in the mid-nineteenth century, and ten specimens each were measured for the remaining three taxa. Variation present within a single specimen was tested by dissecting five flowering heads per plant for the first three specimens of *S. ulmifolia*, *S. nemoralis*, and *S. canadensis*. One specimen of *S. shortii* was analyzed in this manner, with lower sample

←

collection localities of herbarium specimens of *S. canadensis* var. *scabra* (c), *S. nemoralis* (n), *S. ulmifolia* (u), and *S. shortii* (s) sampled for the initial herbarium study. The extirpated population of *S. shortii* is designated by an asterisk. The arrow indicates the area enlarged in part A.

Table 1. List of morphological characters, with abbreviations, analyzed on field and/or herbarium samples of the four *Solidago* taxa and utilized for morphometric analyses. Sample size: *S. shortii* (68), *S. nemoralis* (25), *S. ulmifolia* (25), *S. canadensis* var. *scabra* (25).

Abbreviation	Morphological Character
Continuous Characters	
1. RTUB	Length of ray tube
2. RSTR	Length of ray strap
3. RWID	Width of ray strap
4. LWIP	Distance from widest portion of leaf to leaf apex
5. INVL	Height of involucre
6. PHYW	Width of middle series phyllary
7. DPAP	Length of disk pappus
8. RPAP	Length of ray pappus
9. DCOR	Length of disk corolla
10. LEAL	Length of cauline leaf from the upper plant portion
11. LEAW	Width of cauline leaf from the upper plant portion
12. STOT	Length of ray strap/total length of ray corolla
13. TTOT	Length of ray tube/total length of ray corolla
14. RCOR	Length of ray corolla
15. LWRT	Length of cauline leaf/width of cauline leaf
Discontinuous Characters	
16. INFP	Number of hairs present inside a 0.75 mm ² stem area inside the inflorescence
17. UPPP	Number of hairs present inside a 0.75 mm ² stem area on the upper portion of the plant
18. LEAP	Number of hairs present inside a 0.75 mm ² area on the underside of a leaf in the upper plant portion
19. MDVP	Number of hairs present along a 0.5 mm ² section of the midvein on the lower side of a leaf in the upper plant portion

size due to the limits of specimen availability for such sampling. Characters 5–15 (Table 1) were measured for each head, and the resulting means from each head were compared. This revealed little variation within a single plant, and subsequent analysis included only one head per plant.

The values obtained from this initial herbarium study were analyzed using PCA to identify the characters that exhibited the highest loadings. These informative characters were the focus of analysis in subsequent studies.

Field studies were conducted between September 5 and October 9, 1998. Three leaves and three flowering heads were taken from plants along linear transects in six of the twelve known

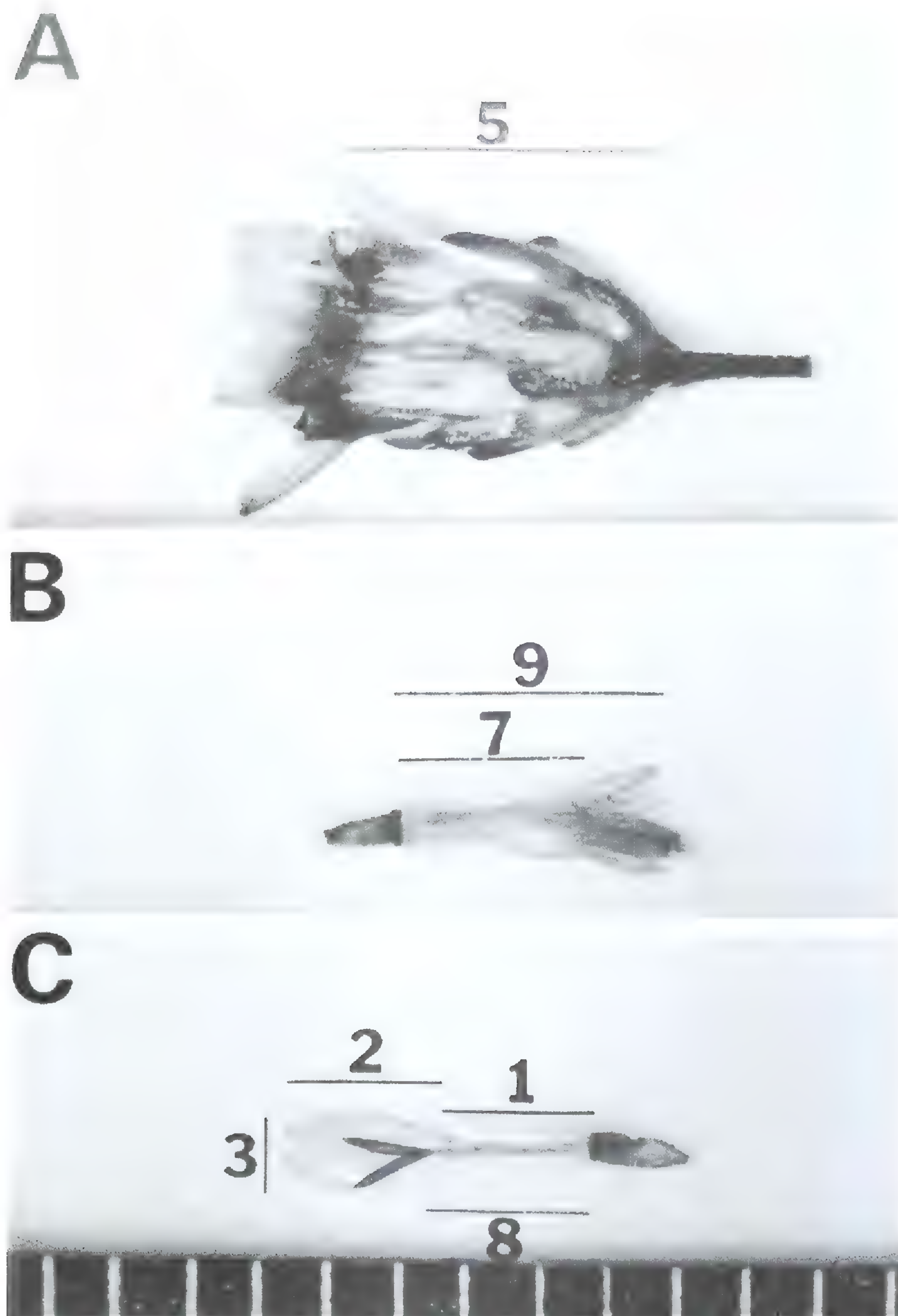


Figure 2. Selected floral characters utilized in the analysis. A. Flowering head of *Solidago shortii*. B. Disk floret. C. Ray (ligulate) floret. Divisions present on bottom bar are in mm. Numbers denoting characters correspond with those in Table 1.

populations (Figure 1A). *Solidago shortii* specimens were sampled from populations #1, 7, 8, 9, 11, and 12; *S. nemoralis* from #4 and 12; *S. ulmifolia* from #7 and 9; and *S. canadensis* var. *scabra* from #4, 9, and 11. Vegetative material was measured fresh, with floral material dried for later analysis. Floral material was re-hydrated in a detergent solution and measured with the aid of a dissecting scope equipped with an optic micrometer. To assess the possibility of alteration of features on herbarium specimens due to drying, fresh vegetative material was measured and subsequently vouchered. Ten specimens were examined one year after preparation, and LEAL (Table 2) was again measured from the dried specimens. Drying of leaf material did result in a small, consistent reduction in leaf length. Dried leaves were on average 97.52% ($n = 10$, $SD = 0.96\%$) of their fresh length. Pertinent vegetative measurements from the FO herbarium specimens were adjusted to take into account this slight shrinkage. All floral material taken fresh from the study sites was dried according to standard herbarium practices before rehydrating and analysis; therefore comparisons with floral material from the herbarium sheets were made without numerical adjustment.

A total of 99 plants (54 *Solidago shortii*, 15 *S. nemoralis*, 15 *S. ulmifolia*, and 15 *S. canadensis* var. *scabra*) were analyzed in the fashion described above. To reduce the possibility of variation due to geographic factors or chromosomal races (Brammell and Semple 1990), individual plants of the latter three taxa were sampled from populations in Kentucky found in proximity or within the populations of *S. shortii*. Seven *S. shortii* herbarium specimens from the extirpated type locality were analyzed with the 54 *S. shortii* specimens sampled from the BL populations. Summary statistics for the 99 field specimens are presented in Table 2.

The data generated from the field study were analyzed with PCA and DFA. In each analysis, characters were excluded to eliminate pairs of characters that were likely genetically redundant (as revealed by high Pearson correlation coefficient values between all possible pairs of characters). The final character suites (along with component loadings) used in the PCA for each pairwise comparison are presented in Table 3. The characters used in DFA were LWIP, INVL, PHYW, RTUB, RSTR, STOT, and RPAP, with four of these (LWIP, RTUB, STOT, and RPAP) log-transformed because they were non-normal. To visualize the results of the PCA, the components exhibiting the highest loadings

Table 2. Means $\pm$ SD and ranges for morphological characters measured for the four *Solidago* taxa at Blue Licks. Character abbreviations are defined in Table 1. All measurements are in mm, except LEAL, LEAW, and LWIP, which are in cm. n = sample size. *n = 5 for LEAL, LEAW, LWIP.

Character	<i>S. shortii</i> (n = 54)	<i>S. nemoralis</i> (n = 15)	<i>S. ulmifolia</i> (n = 15)	<i>S. canadensis</i> var. <i>scabra</i> (n = 15)*
LEAL	2.0 $\pm$ 0.891 (0.44–4.38)	1.1 $\pm$ 0.345 (0.6–1.79)	4.4 $\pm$ 1.102 (2.44–6.94)	4.5 $\pm$ 0.740 (3.42–5.31)
LEAW	0.5 $\pm$ 0.962 (0.038–1.0)	0.3 $\pm$ 0.096 (0.17–0.52)	1.1 $\pm$ 0.349 (0.520–1.870)	0.7 $\pm$ 0.142 (0.50–0.89)
LWIP	1.0 $\pm$ 0.535 (0.089–2.6)	0.4 $\pm$ 0.152 (0.18–0.77)	2.3 $\pm$ 0.527 (1.41–3.35)	2.8 $\pm$ 0.590 (1.90–3.31)
INVL	4.6 $\pm$ 0.473 (3.6–5.5)	4.0 $\pm$ 0.279 (3.5–4.4)	3.5 $\pm$ 0.460 (3.0–4.3)	3.9 $\pm$ 0.493 (3.0–4.5)
PHYW	0.9 $\pm$ 0.109 (0.7–1.2)	0.7 $\pm$ 0.070 (0.6–0.8)	0.7 $\pm$ 0.108 (0.5–0.9)	0.5 $\pm$ 0.086 (0.4–0.7)
DCOR	3.6 $\pm$ 0.301 (2.9–4.4)	3.0 $\pm$ 0.262 (2.3–3.3)	2.7 $\pm$ 0.242 (2.1–3.0)	3.6 $\pm$ 0.304 (3.1–4.0)
RTUB	1.8 $\pm$ 0.261 (1.2–2.4)	1.8 $\pm$ 0.263 (1.4–2.3)	1.2 $\pm$ 0.158 (0.9–1.4)	2.1 $\pm$ 0.255 (1.8–2.7)
RSTR	2.1 $\pm$ 0.306 (1.5–3.0)	1.5 $\pm$ 0.216 (1.1–1.8)	1.5 $\pm$ 0.292 (1.1–2.1)	1.7 $\pm$ 0.379 (1.0–2.3)
STOT	0.552 $\pm$ 0.044 (0.455–0.688)	0.456 $\pm$ 0.027 (0.406–0.5)	0.561 $\pm$ 0.028 (0.520–0.618)	0.437 $\pm$ 0.055 (0.333–0.537)
RWID	0.9 $\pm$ 0.133 (0.6–1.2)	0.6 $\pm$ 0.070 (0.5–0.7)	0.7 $\pm$ 0.18 (0.4–1.1)	0.3 $\pm$ 0.106 (0.1–0.5)
RPAP	2.5 $\pm$ 0.286 (1.8–3.3)	2.2 $\pm$ 0.210 (1.8–2.6)	1.7 $\pm$ 0.240 (1.3–2.2)	2.7 $\pm$ 0.429 (1.9–3.6)

Table 3. Characters, with loadings for each principal component, used in comparisons of *Solidago* species pairs in Principal Components Analysis. Character abbreviations are defined in Table 1.

Species Comparison	Character	Component Loading (1)	Component Loading (2)
<i>S. shortii</i> / <i>S. nemoralis</i>	LWIP	0.483	−0.414
	INVL	0.782	0.293
	RTUB	0.013	0.891
	RSTR	0.896	0.122
	STOT	0.762	−0.552
	RWID	0.712	0.017
	RPAP	0.726	0.357
<i>S. shortii</i> / <i>S. canadensis</i> var. <i>scabra</i>	INVL	0.754	0.286
	DCOR	0.398	0.848
	RTUB	−0.392	0.869
	RSTR	0.864	0.327
	STOT	0.877	−0.368
	RWID	0.822	−0.210
<i>S. shortii</i> / <i>S. ulmifolia</i>	LWIP	−0.667	0.626
	PHYW	0.770	−0.001
	RTUB	0.846	−0.053
	RSTR	0.807	0.051
	RWID	0.645	0.655

were plotted against each other in a graphical manner (Figures 3–5). For the DFA, factors 1 and 2 were plotted against each other in the same fashion (Figure 6). All statistical analyses of data were performed using SYSTAT version 5.2 (1992, SPSS Inc., Evanston, IL) on an Apple Power Macintosh computer containing a G3 processor.

RESULTS

Species circumscription. Plants with paniculate inflorescences; tri-nerved, glabrous leaves; fewer than 8 ray florets; and involucre greater than 3.5 mm in length formed a clear morphological unit that encompassed the range of variation present in both the BL and FO *Solidago shortii* specimens. Whole-plant comparisons also revealed the characters most useful in pairwise comparisons between *S. shortii* and each of the other species examined. *Solidago shortii* had fewer (5–7 vs. 8–13) and broader

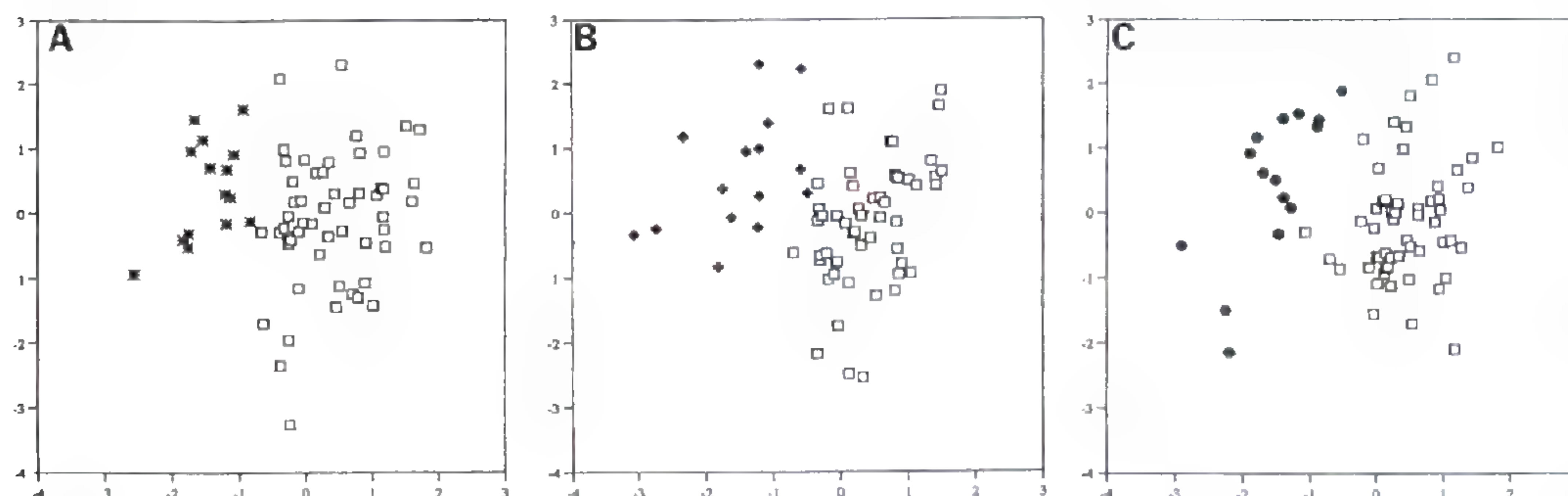


Figure 3. Scattergrams showing results of Principal Components Analysis for interspecific comparisons. Panels A, B, and C show pairwise comparisons between individual plants of *Solidago shortii* from the Blue Licks population (rectangles) and individuals of *S. nemoralis* (stars), *S. canadensis* (diamonds), and *S. ulmifolia* (circles), respectively. Factor 1 is plotted along the abscissa, Factor 2 along the ordinate.

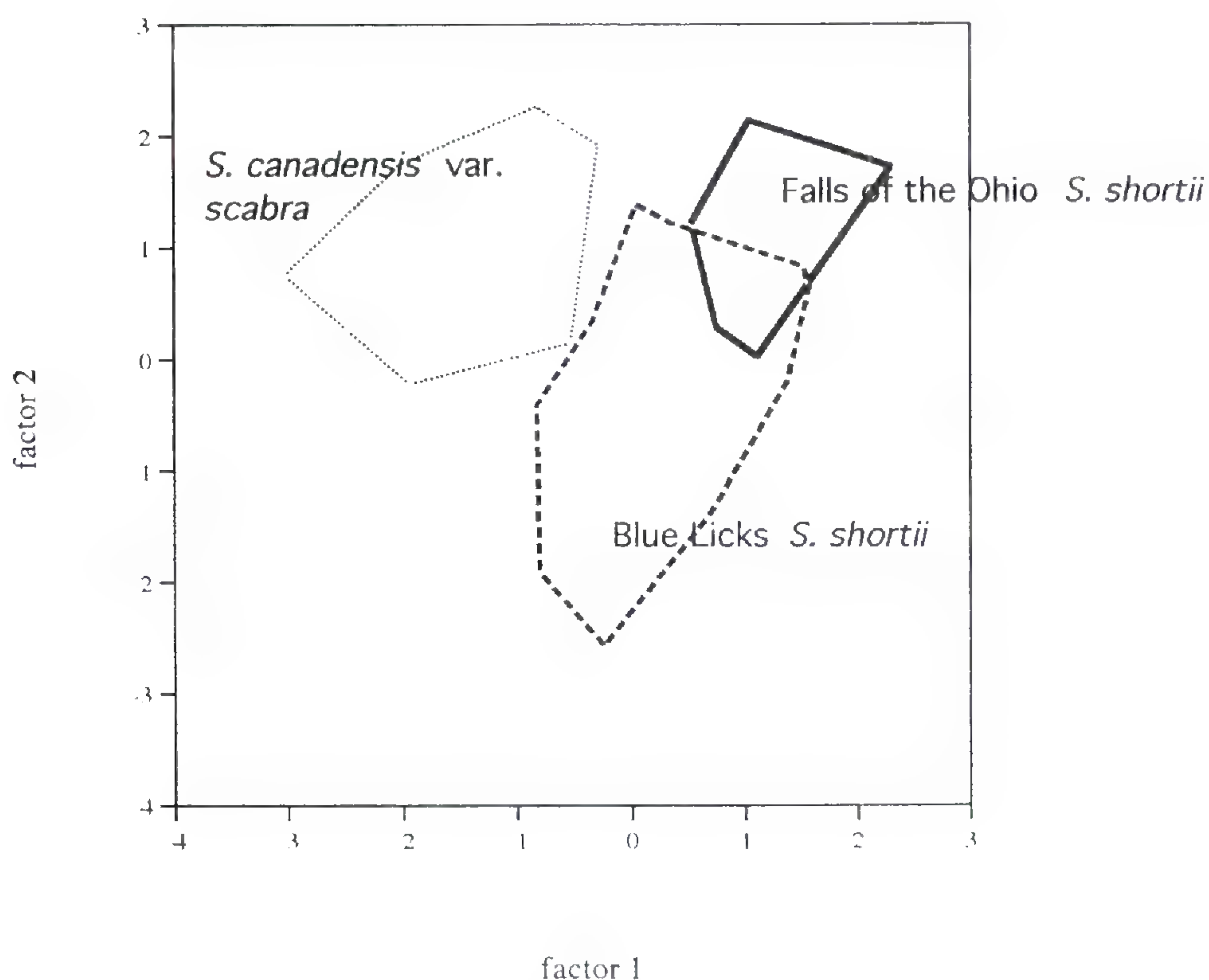


Figure 4. Scattergram showing results of the Principal Components Analysis of *Solidago shortii* in comparison with *S. canadensis* var. *scabra*. The species' polygons are demarcated by individual specimens of each respective taxon sampled herein; for clarity, the individual specimens have been omitted from the figure. The extant Blue Licks and extirpated Falls of the Ohio populations of *S. shortii* are indicated by their respective polygons.

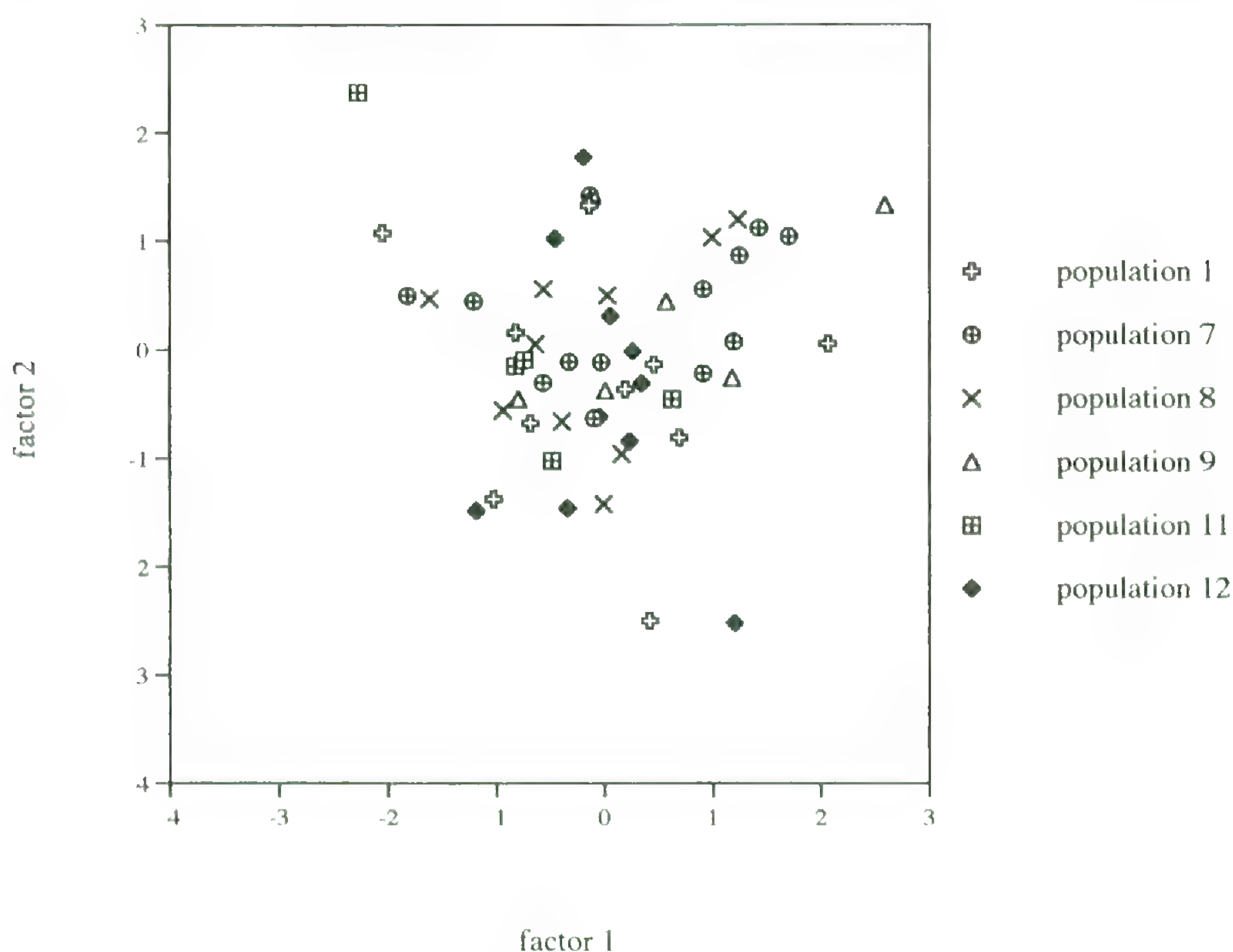


Figure 5. Intergroup variation present within *Solidago shortii* from Blue Licks and vicinity, Kentucky. Each set of identical symbols represents individuals from a single population; in all, six populations are shown.

(0.6–1.2 vs. 0.1–0.5 mm) ray florets relative to *S. canadensis* var. *scabra*. *Solidago shortii* also exhibited glabrous leaves, while the leaves of *S. canadensis* var. *scabra* were densely pubescent. Short's goldenrod exhibited fewer (5–7) rays relative to *S. leavenworthii* (10–16). *Solidago shortii* had fewer (5–7 vs. 7–15) ray florets than *S. gigantea*, and the sub-inflorescence stem of *S. shortii* was pubescent, compared to the glabrous sub-inflorescence stem of *S. gigantea*. Short's goldenrod had a longer involucre (3.6–5.5 vs. 2.5–4.0 mm) relative to *S. tortifolia*. The width of the largest leaves of *S. shortii* (> 1.0 cm) were also diagnostic relative to those of *S. tortifolia* (< 1.0 cm). *Solidago shortii* had a longer involucre (3.6–5.5 mm) than *S. rupestris* (2.0–3.1 mm). Pubescence characters best differentiated *S. shortii* from *S. ulmifolia*. *Solidago shortii* had a pubescent sub-inflorescence stem and glabrous abaxial leaf midveins, relative to the glabrous sub-inflorescence stems and pilose abaxial leaf midveins of *S. ulmifolia*. *Solidago shortii* had wider (0.6–1.2 vs. 0.5–0.7 mm) ray florets relative to *S. nemoralis*. The glabrous leaves of Short's

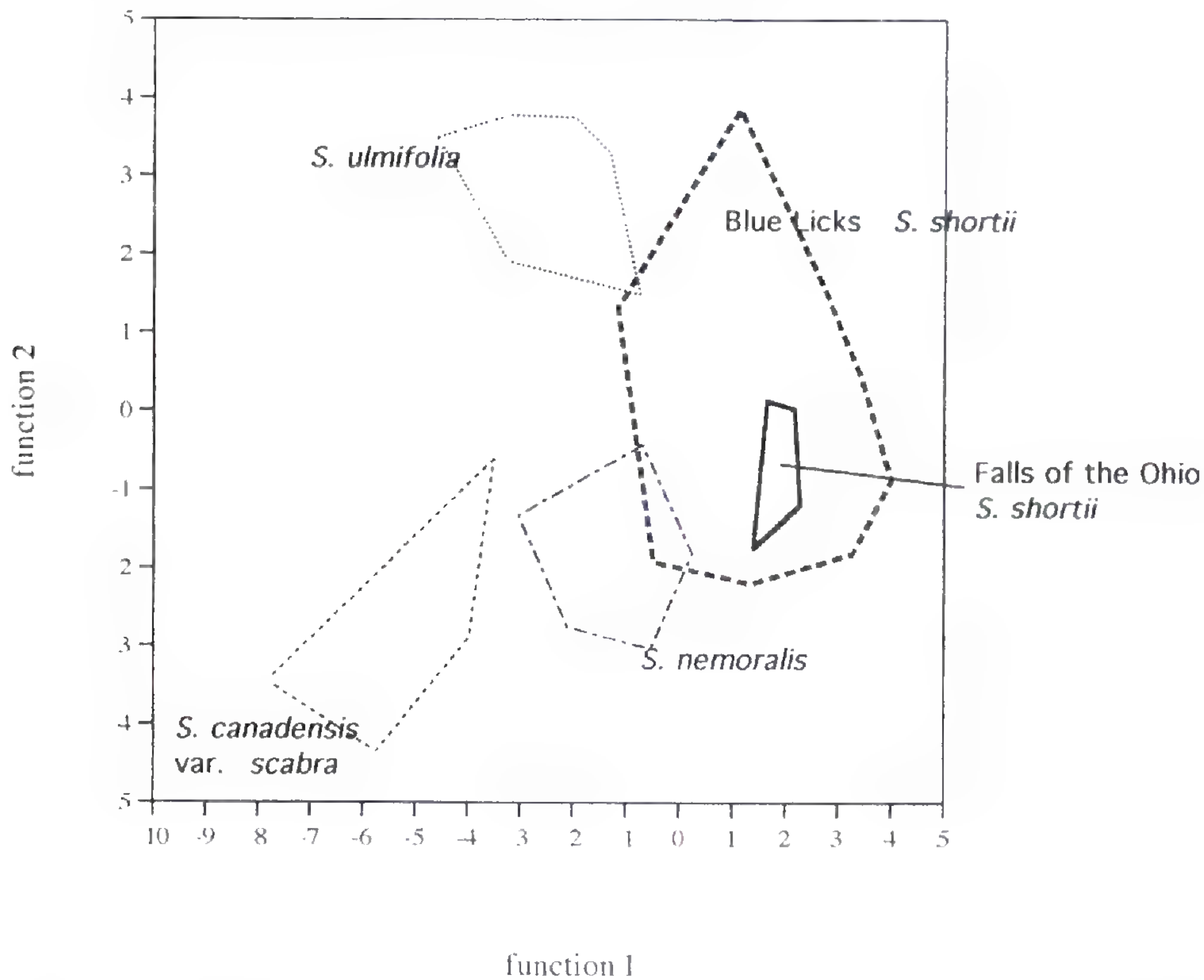


Figure 6. Scattergram representing the Discriminate Function Analysis of all species considered in the morphometric analysis. The species' polygons are demarcated by individual specimens of each respective taxon sampled herein; for clarity, the individual specimens have been omitted from the figure. The extant Blue Licks and vicinity, and extirpated Falls of the Ohio populations of *Solidago shortii* are indicated by their respective polygons.

goldenrod also helped distinguish it from *S. nemoralis*, which exhibited densely puberulent leaves.

All *Solidago shortii* specimens from the BL populations were grouped with the FO specimens using these criteria. In addition, the first plants taken from the Blue Licks area in 1939 were annotated as *S. shortii* by M. L. Fernald and others following review alongside the original FO material archived at the Gray Herbarium (Braun 1941). The morphometric analysis also supported the idea that the BL and FO specimens belong to the same taxon. The BL and FO *S. shortii* specimens, in pairwise comparisons with *S. canadensis* var. *scabra*, *S. nemoralis*, and *S. ulmifolia*, consistently formed a distinct cluster segregate from those clusters formed by the other taxa (Figure 3A–C). Furthermore, when viewed as distinct clusters, the specimens of Short's goldenrod from the Falls of the Ohio and from Blue Licks formed two overlapping clusters that segregated from *S. canadensis* var. *sca-*

bra (Figure 4), a close phylogenetic relative in subsect. *Triplinervae* (Semple et al. 1999). The DFA also provided evidence of the unity of the BL and FO specimens. When treated as separate *a priori* groups, the cluster formed by the FO specimens was completely imbedded within the BL cluster (Figure 6). In addition, 4 of the 54 BL *S. shortii* specimens were misclassified as belonging to the FO *a priori* group.

Species variation. Of interest were the relative amounts of morphological variation present at the Blue Licks study sites in three common *Solidago* species compared to *S. shortii*. Short's goldenrod is known only from the aforementioned sites, therefore our sample area was restricted to them. The common *Solidago* species exhibit cytological and/or geographic races throughout their range of occurrence (Brammell and Semple 1990; Cronquist 1980). Sampling only from the Blue Licks sites excluded the morphological variation which results.

The scales on the PCA graph axes (Figures 3–5) are relative. Therefore, comparisons within and among the graphs can be made. In these graphs the area occupied by a group of sampled individuals of the same species was directly related to the amount of measured morphologic variability. *Solidago shortii* occupied a considerably larger area than *S. nemoralis* and an area comparable to that of *S. canadensis* var. *scabra*, reflecting an equal or greater degree of morphologic variability relative to these two taxa (Figure 3A, B). The area occupied by *S. ulmifolia* was slightly larger than that occupied by *S. shortii* (Figure 3C), indicating that the sampled specimens of *S. ulmifolia* exhibited a slightly higher degree of morphologic variability. Of some concern were the relatively small sample sizes (15 each) present for the three common species. In order to investigate the effects of sample size, data sets were formed using the 15 samples of each of the common species (*S. canadensis* var. *scabra*, *S. nemoralis*, and *S. ulmifolia*) combined with 15 *S. shortii* samples taken from identical populations as the common species. These two data sets were analyzed in the same manner as the large sets, and similar variational ranges were observed (data available upon request from J.B.B.). The rare *S. shortii* exhibited a comparable or greater extent of phenotypic variability than two of the three common species to which it was compared from the BL study area.

Population variation. The level of intra- and interpopulational variation within *Solidago shortii* from Blue Licks was significant. Although all of the sampled BL populations overlapped, several of the populations (#1, 9, 11, and 12) contained individual specimens that were extreme outliers (Figure 5).

DISCUSSION

Solidago shortii was first collected by Dr. C. W. Short from Rock Island at the Falls of the Ohio River, Louisville, Kentucky, in 1840 (Beck et al. 1999). This site was destroyed by inundation upon the construction of the McAlpine Locks and Dam in the 1920s (Baskin et al. 1986). The occurrence of the species at the Blue Licks locality was reported by Braun (1941), and is the only known occurrence of the species (Buchele et al. 1989; Evans 1987). One possible reason for the limited distribution of this species is its possible dependence on disturbance by migrating eastern woodland American bison (Braun 1941). Upon extirpation of the bison, Short's goldenrod may have experienced a concomitant decline, due perhaps to increased competition from both native and invasive plant species (Buchele et al. 1989).

Whole-plant comparisons with both closely related and sympatric goldenrod species indicate that *Solidago shortii* is a distinct taxon, and morphometric comparisons between *S. shortii* and a subset of these species provides supporting evidence. These two approaches provide even stronger evidence to support the taxonomic contention that the BL populations are indeed *S. shortii* as described from the FO material. Though the results of both PCA and DFA indicate that plants from BL and FO are taxonomically identical, the placement of specimens of *S. shortii* from these two locations differ in the two analyses. The FO specimens are completely embedded in the cluster of BL specimens in the DFA plot (Figure 6). On the PCA plot, however, FO specimens appear at the end of the BL cluster and only partially overlap the BL specimens (Figure 4). Two factors account for the discrepancy between the DFA and PCA results. First, different characters were included in DFA and PCA, since different taxa were included in these analyses. Second, more taxa were included in the DFA than the PCA. The inclusion of more taxa in a DFA or PCA requires the simultaneous analysis of more sets of diagnostic characters, with the resultant diminishment of resolution between adjacent

specimen clusters. Thus, the FO specimens appear more different from the BL specimens on the PCA plot than they do on the DFA plot because, on the PCA, FO and BL are being compared with only one other *Solidago* taxon (vs. three other taxa on the DFA plot). Differences do exist, however, between the BL and FO specimens of *S. shortii*. Plants from FO tended to have larger leaves and capitular structures (disk corollas, ray pappus bristles, and involucre) than BL plants. Relative to the characters that distinguish *S. shortii* from other *Solidago* species, these differences between BL and FO plants are slight and do not justify treating FO as a different taxon than BL.

The morphological distinction could be due to spatial or temporal factors, or both. Temporal factors would likely entail subsequent genetic and morphological divergence over time between specimens collected from 1839–1842 from the Falls of the Ohio River and specimens collected at Blue Licks from 1939–present. Spatial factors would involve past restricted gene flow due to geographic distance (approximately 160 km) between the two localities. Another intriguing possibility is that of past differential gene flow to the separate populations of *Solidago shortii* (FO and BL) from taxa with close phylogenetic affinity (Nesom, pers. comm.). *Solidago shortii* is placed in subsection *Triplinervae* with three other species found in Kentucky—*S. canadensis* var. *scabra*, *S. gigantea*, and *S. rupestris*—and with two species from the southeastern U.S. (*S. leavenworthii* and *S. tortifolia*; Nesom 1993). Although only *S. canadensis* var. *scabra* is presently found within proximity of *S. shortii*, it is possible that in the post-Pleistocene landscape one or more of the above taxa might have been in close proximity to *S. shortii* at either FO or BL, and gene flow events could have contributed to the phenotypic variation seen between these populations. Given the dynamic nature of the vegetational changes in the post-Pleistocene environment of Kentucky and the eastern U.S. (Whitehead 1973; Wilkins et al. 1991; Wright 1976), it is plausible that distributional shifts in vegetation types and species allowed, at some point in time, for sympatric gene flow between sister taxa and *S. shortii*. The testing of this hypothesis would require the development of suitable molecular markers to allow for the dissection of the genome of *S. shortii* to determine if elements of other *Solidago* spp. genomes are present within Short's goldenrod.

The highly variable phenotype of this endemic species was first

observed among the initial collections of the plant by Dr. C. W. Short in 1839. Asa Gray, the species author of *Solidago shortii*, made note of morphological variation within the species in his original circumscription of the taxon from specimens obtained from Short. He noted two “varieties,” designated β and γ , that differed from “typical” *S. shortii* specimens. However, he felt the extent or constancy of this variation was insufficient to warrant the formal designation of these entities as discrete taxa. It is remarkable that Gray noted this variation in a sample size of less than 10 specimens, from material collected at or near the Falls of the Ohio locality (Beck et al. 1999). Gray’s observations do provide an independent qualitative assessment of the morphological variability found within the species.

A prevailing paradigm of rare and endangered species is that they often exhibit markedly decreased levels of phenotypic variability, as evidenced by limited ecological tolerances, homogeneous morphology, or genetic homozygosity. This study has shown a remarkable level of phenotypic variability in a species known from a single locality presently represented by perhaps several thousand individual plants.

There are four explanations that could account for the morphological variability found within Short’s goldenrod. First, the variability could be due to epigenetic phenotypic plasticity, caused by external environmental influences. Among these could be edaphic factors, water relations, relative incipient solar radiation, and topographic influences (Tilman 1982, 1988). An exhaustive analysis by Buchele et al. (1989) revealed no striking differences among the habitats from which plants were sampled for this study.

The second possibility is that the inter- and intrapopulational differences have a genetic basis, and are due to the presence of different allelic and genic combinations within different individuals and populations. If gene flow between populations is restricted or nonrandom, then specific genetic differences could be established and maintained. Furthermore, if clonal reproduction is predominant over sexual reproduction, as has been suggested (Buchele et al. 1989), then the lack of meiotic recombination would maintain specific phenotypes over time. One would expect with the small numbers of individuals seen in some populations of *Solidago shortii*, that genetic drift would lead to a reduction of variation (Hastings 1997) within the smaller populations (e.g.,

#8, 11, 12). However, these three populations, whose numbers of stems ranged from 7-fold to 24-fold less than those of population #1, all showed a similar extent of variability. It should be noted that, due to the clonal nature of reproduction of *Solidago*, the number of stems noted above is not an indication of the number of plants, and we are assuming a direct correlation between the number of individual ramets in the population and the number of specific genets.

A third possibility is the production of hybrid offspring between *Solidago shortii* and one or more of the congener taxa at Blue Licks, due to cross-pollination. Interspecific hybridization has been suggested to occur in the genus (Cronquist 1980; Fernald 1970) and between members of different sections (Nesom 1993). There is, however, no direct experimental evidence that supports this possibility. The perceived gradation of the Blue Licks *S. shortii* plants toward the other *Solidago* taxa is thus interpreted as infraspecific variation. We have not been able to designate any specimens as being of hybrid origin through our statistical analyses. Two of the major insect associates of *S. shortii* flowers are the goldenrod soldier beetle (*Cauliognathus pennsylvanicus*) and the black blister beetle (*Epicauta pennsylvanica*; Buchele et al. 1992b). The soldier beetle exhibits a low frequency of movement between neighboring plants, which probably reduces the efficacy of cross-pollination and gene flow between adjacent individuals. The blister beetle is a flower predator, which could also reduce the readiness of pollinators to visit flowers harboring the beetle (Gross and Werner 1983).

The fourth possibility is that the level of variability we observed in *Solidago shortii* relative to the more common species is simply an artifact of the suite of characters we chose. Further studies should include either an expanded set of morphological characters, or the use of suitable molecular markers.

At present we lack evidence that provides unequivocal support for any of the four possibilities described above. However, our analyses do indicate that the sampled populations of *Solidago shortii* do not represent a homogeneous cluster, but rather an amalgam of different phenotypes.

The findings described here have implications for management of *Solidago shortii*. Given the level of morphological variability among populations, a rigorous genetic profile needs to be obtained from individuals of different populations at Blue Licks. If

the morphologic variability is mirrored at the genetic level, then each population could possess a profile distinct from other populations. Efforts at reintroduction of the species into former localities (i.e., the Falls of the Ohio River) or introduction into new habitats (perhaps along remnants of former bison traces) would need to take into account the nature of the variability, and the suitability of specific populations as sources of transplant material.

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A MUSCOIDES-LIKE *FUCUS* FROM A MAINE SALT
MARSH: ITS ORIGIN, ECOLOGY, AND
TAXONOMIC IMPLICATIONS

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ABSTRACT. The morphology and habitat of a dwarf moss-like or muscoides-like fucoid brown alga were studied in the Brave Boat Harbor salt marsh of York-Kittery, Maine, U.S.A. using transect studies and transplant experiments. The plant, which lacks a holdfast, forms a dense embedded turf amongst sparse *Spartina patens* populations in the high marsh, particularly on well-drained sandy sediments near the Harbor's mouth. The plant's dichotomously branched fronds were smaller than those previously reported for muscoides-like populations from Europe (mean = 13.2 mm long, 1.1 mm wide, and 0.1 g damp-dried weight), while they had a similar dominance of marginal hair pits or cryptostomata. Transplantation of *in situ* *Fucus spiralis* from the lower to the upper marsh resulted in enhanced fragmentation, stunting, proliferation, and reduced reproduction. Reciprocal transplantation of the muscoides-like *Fucus* from upper to lower elevations caused enhanced frond length and proliferation. Based upon detailed transplant and morphological studies, we conclude that the muscoides-like *Fucus* plants from Brave Boat Harbor represent a phenotypic variant of *F. spiralis*, caused by detachment, extensive proliferation, and subsequent degeneration of detached fragments. The plant's dwarf morphology is primarily linked to a series of unique environmental conditions (desiccation and low nutrients), plus the type of attached parental material available. Thus, the dwarf muscoides-like *Fucus* in Europe and some Northwest Atlantic sites may be derived from *F. vesiculosus*, while in Brave Boat Harbor the parental material is *F. spiralis*. An analogous pattern is also evident between *Ascophyllum nodosum* and its detached ecad *scorpioides*, with the presence of dwarf specimens and the occurrence of a conspicuous morphological continuum between the two plants.

Key Words: Brave Boat Harbor Maine, ecad ecology, fucoid algae, salt marsh algae, seaweed development, taxonomy

Seaweeds that lack holdfasts (free-living) are common throughout the world, particularly within protected embayments, salt marshes, and estuaries (Norton and Mathieson 1983). The temperate North Atlantic fucoid genera *Ascophyllum* and *Fucus* contain several free-living salt marsh plants (Baker and Bohling 1916; Fritsch 1945; Niell et al. 1980), which can contribute major quantities of biomass and primary productivity (Brinkhuis 1976;

Brinkhuis and Jones 1976; Brinkhuis et al. 1976; Chock and Mathieson 1976). Several positive interactions occur between salt marsh flowering plants and unattached fucoids, including reduced desiccation and enhanced survival of *A. nodosum* (L.) Le Jolis ecad *scorpioides* (Hornemann) Reinke, plus increased cordgrass biomass (*Spartina alterniflora* Loisel.) due to enhanced sediment nutrients (Chapman and Chapman 1999; Gerard 1999). The taxonomy of unattached fucoids is poorly understood (Fritsch 1945; Norton and Mathieson 1983; Sears 1998), with plants being variously classified as ecads, megaecads, species, and varieties (Baker and Bohling 1916; Sears 1998; Taylor 1957; Wynne and Magne 1991). The “altered” morphology of free-living fucoids, which includes dwarfing, spiral twisting, profuse branching, vegetative propagation, and the lack of a holdfast (Baker and Bohling 1916; Fritsch 1945; Niell et al. 1980; Norton and Mathieson 1983) has contributed to these taxonomic problems. The varied morphologies of free-living fucoids have been attributed to reduced nutrients and/or salinities, sluggish currents, and enhanced desiccation (Boney 1966; Chapman 1964). In discussing the origin of free-living fucoids Fritsch (1945) emphasizes that they “are all derived by vegetative propagation from saxicolous types.”

One of the most unique marsh fucoids is the dwarf, embedded moss-like *Fucus* that is frequently found within upper salt marshes of Europe and the British Isles. It is described as being 5–6 cm tall, having cylindrical to compressed branches (1–3 mm wide), and bearing marginal hair pits or cryptostomata (cf. Fritsch 1945; Jorde 1966; Lynn 1935; Newton 1931; Valera and Cooke 1979). Although lacking a holdfast, the plant is anchored (i.e., partially embedded) in firm sand or peat-like sediments within high tidal marshes (Cotton 1912; Feldmann and Magne 1964; Lynn 1935; Norton and Mathieson 1983). Muscoides-like *Fucus* plants have been variously designated as varieties (Cotton 1912; Lynn 1935), ecads (Baker and Bohling 1916; Niell et al. 1980), or as distinct species (Feldmann and Magne 1964; Parke and Dixon 1976; Wynne and Magne 1991). In Cotton’s (1912) initial characterization of this muscoides-like *Fucus*, he treated it taxonomically as *F. vesiculosus* L. var. *muscoides* and described it as forming moss-like carpets (i.e., swards) within the high intertidal zone at Clare Island, Ireland. Subsequently Baker and Bohling (1916) designated the plant as *F. vesiculosus* ecad *muscoides*,

emphasizing that it was part of a morphological cline within the megaecad *limicola* Baker *et* Bohling (Clements 1905); the ecads *caespitosus* Baker *et* Bohling, *filiformis* J. Agardh, *nanus* J. Agardh, *subecostatus* J. Agardh, and *volubilis* (Hudson) Turner were also included within the megaecad *limicola* of *F. vesiculosus*. Feldmann and Magne (1964) elevated *F. vesiculosus* var. *muscoides* to a distinct species, *F. muscoides*. On the other hand, during a recent survey of Spanish *F. vesiculosus* populations, Niell *et al.* (1980) agreed with Baker and Bohling's (1916) interpretation, designating various ecads within *F. vesiculosus* megaecad *limicola* and showing a gradation of morphology ranging from *F. vesiculosus* f. *axillaris* to *F. vesiculosus* ecads *volubilis*, *caespitosus*, and *muscoides*.

Wynne and Magne (1991) also agreed with Feldmann and Magne (1964), stating that this plant should be recognized at the species level. However, they pointed out that the name employed by Feldmann *et* Magne (1964), namely *Fucus muscoides* (Cotton) Feldman and Magne, created a later homonym of a red alga now known as *Acanthophora muscoides* (L.) Bory de Saint-Vincent (1828). Accordingly they proposed a new name, *F. cottonii* M. J. Wynne *et* Magne, in honor of A. D. Cotton, suggesting that the dwarf morphology and unique ecological niche within high tidal marshes clearly delineated the taxon.

The present study was undertaken after a floristic investigation of seaweeds within Brave Boat Harbor, York-Kittery, Maine, U.S.A. (Figure 1) revealed the first occurrence of a muscoides-like *Fucus* plant in North America (Mathieson *et al.* 2001). In the present account we summarize detailed morphological, ecological, and transplant data regarding these unique populations, in order to clarify the plant's origin, taxonomy, and biology.

MATERIALS AND METHODS

Mathieson *et al.* (2001) have given a detailed characterization of the Brave Boat Harbor salt marsh (43°06.0'N, 70°39.33'W; hereafter BBH), including its geography, hydrographic conditions (temperature and salinity), habitat variability, species composition, and site locations within the main tidal channel and four contiguous tidal tributaries. The biomass patterns for the muscoides-like *Fucus* and other salt marsh plants were recorded at seven transect sites along the main tidal channel (Figure 1), with

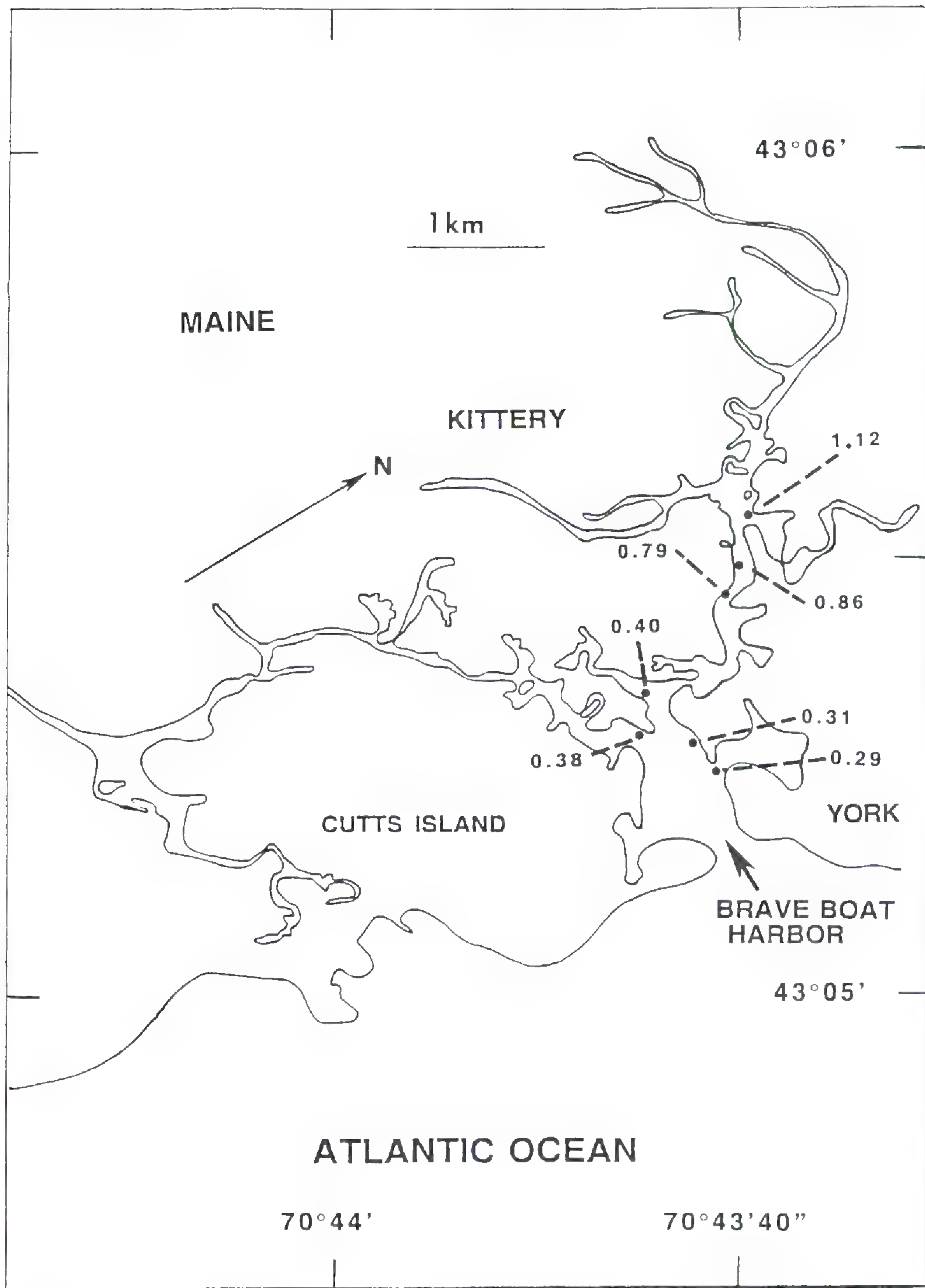


Figure 1. Brave Boat Harbor, York-Kittery, Maine showing the location of seven transect sites within the main tidal channel. See Figure 1 in Mathieson et al. (2001) for details of the southern Maine coast.

Table 1. Distribution and mean biomass of dominant seaweeds and flowering plants on seven transects within Brave Boat Harbor, Maine. Symbols: % = percent occurrence, × = present, and mean biomass = g dry wt./m² ± 1 SD (± 1 SE).

Site # Distance inland from mouth (km)	1 0.29	2 0.31	3 0.38	4 0.40	5 0.79	6 0.86	7 1.12	%	Mean Biomass (sites present)
SEAWEEDES									
<i>Ascophyllum nodosum</i> (L.) Le Jolis	×						×	28.6	20.5 ± 14.8 (10.6)
<i>Ascophyllum nodosum</i> (L.) Le Jolis									
<i>ecad scorpioides</i> (Hornemann) Reinke		×	×	×	×	×	×	85.7	868.2 ± 1255.0 (500)
<i>Fucus</i> sp. “muscoides-like”	×	×	×	×	×	×	×	100	266.3 ± 122.3 (46.2)
<i>Fucus spiralis</i> L.	×	×	×	×	×	×		85.7	327.8 ± 395.0 (161.4)
<i>Fucus spiralis</i> L.									
<i>ecad lutarius</i> (Kützinger) Sauvageau		×						14.3	130.0 ± 94.8 (94.8)
<i>Fucus vesiculosus</i> L.									
<i>ecad volubilis</i> (Hudson) Turner						×	×	28.6	647.8 ± 590.8 (341.5)
<i>Melanosiphon intestinalis</i> (D. A. Saunders)	×	×	×	×				57.1	378.6 ± 124.0 (62.0)
M. J. Wynne	×	×	×	×	×	×	×	100	112.6 ± 108.8 (41.1)
<i>Rhizoclonium riparium</i> (Roth) Harvey	×	×	×	×	×	×	×	100	112.6 ± 108.8 (41.1)
<i>Vaucheria</i> spp.									
TOTAL SEAWEEDES/SITE	6	7	6	6	6	5	6		

these sites varying from 0.29 km to 1.12 km inland from the mouth. Elevation records were determined using a line level and a surveying rod (Dawes 1998; Mathieson et al. 1998), with vertical heights above or below mean low water (i.e., MLW) being calculated from predicted tidal levels (Harbor Master Program, Version 3, Zihua Software, Marlboro, CT). The delay in tidal rise for inner transect sites was calculated by subdividing the main channel into four 15-minute increments that matched the one-hour delay noted at the innermost part of the marsh.

Transect studies (Figure 1) were conducted between May and September, 1998 at seven sites. Metered lines of variable lengths (5–7 m), depending upon shore topographies, were established at right angles to the shoreline, extending from the tidal channel to the high marsh community dominated by *Spartina patens* (Aiton) Muhl. A minimum of two biomass cores per meter were taken along each transect with a polyvinylchloride tube (95 cm²), particularly when conspicuous vegetational changes occurred or where the muscoides-like *Fucus* was evident. Each core was labeled and returned to the laboratory within one hour where it was stored at 10°C until being processed. Ultimately the macroalgae and salt marsh plants within each core were separated and their damp-dried biomass values converted to g dry wt./m² using a wet to dry weight conversion determined for each species. A comparison of species composition and mean biomass for the seven transects is summarized (Table 1). Morphological assessments of five of the six fucoid taxa found were made, including *Fucus spiralis* L., *Ascophyllum nodosum* (L.) Le Jolis ecad *scorpioides* (Hornemann) Reinke, *F. spiralis* ecad *lutarius* (Kützinger) Sauvageau, *F. vesiculosus* L. ecad *volubilis* (Hudson) Turner, and the muscoides-like *Fucus* (Figures 2 and 3).

Reciprocal transplants of cores (92 cm²) containing *Fucus spiralis* and muscoides-like *Fucus* plants were initiated during June 1998 at a site located 0.38 km inland from the mouth along the main tidal channel of BBH. Vertical transfers were made from +2.0 to +3.4 m above MLW and vice versa, with four different types of populations being assessed: (1) high *in situ* populations of muscoides-like *Fucus* or a mixture of fragmented *F. spiralis* ecad *lutarius* and muscoides-like plants; (2) low *in situ* *F. spiralis*; (3) low transplants or plants that were transferred from the higher to the lower fucoid zone; and (4) high transplants or plants that were transferred from the lower to the higher fucoid zone.

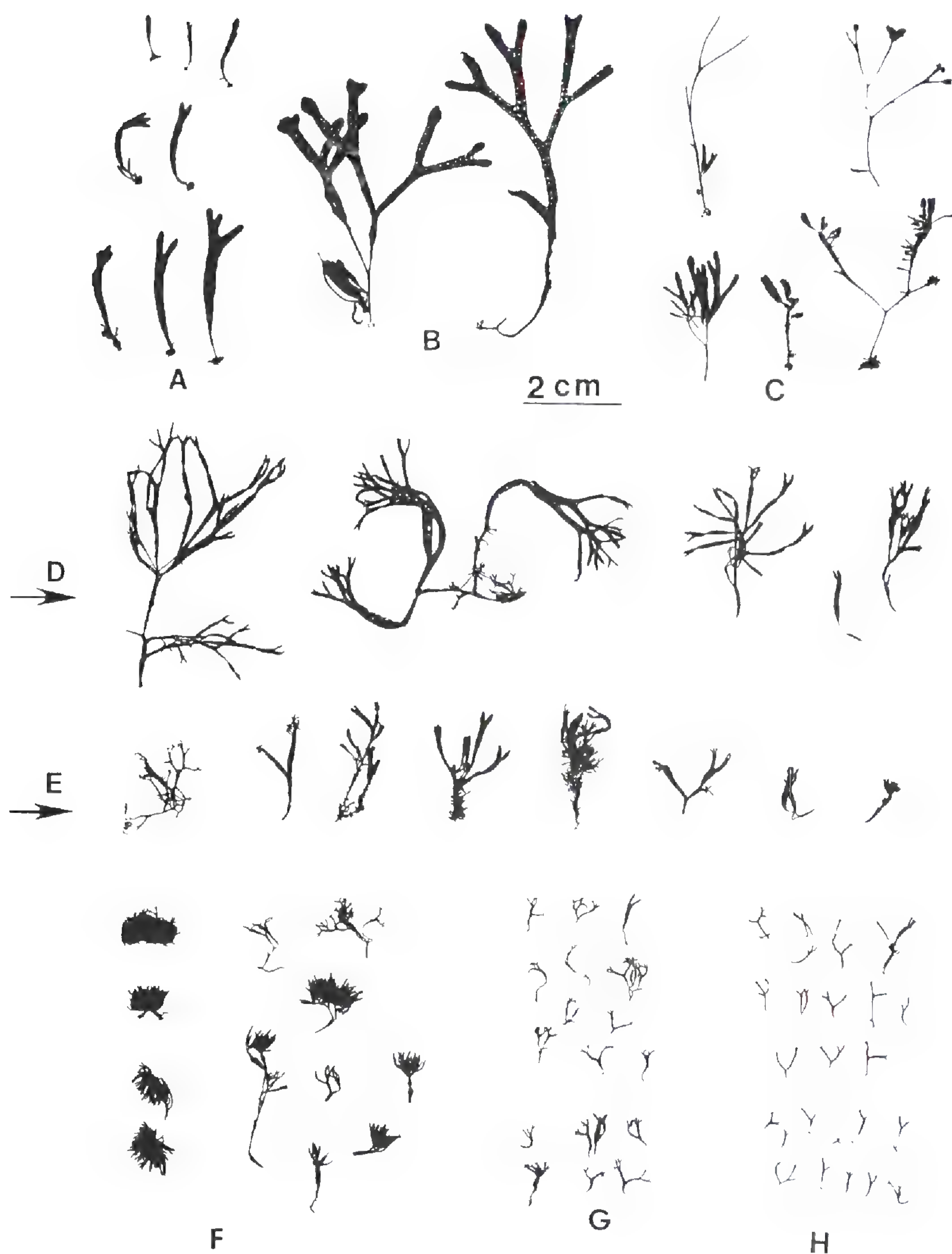


Figure 2. Silhouettes of morphological variability in three fucoid populations from Brave Boat Harbor. Attached *Fucus spiralis* ranging from germlings (A, group of 8), to a pair of reproductively mature adults (B), to residual and proliferous specimens (C, group of 5). Detached specimens of *F. spiralis* ecad *lutarius* grading from large, fragmented fronds (D, group of 5), to more proliferous, smaller plants (E, group of 8). Turf-like populations of muscoides-like *Fucus* ranging from tufted, elongated specimens (F, group of 12), to short, individual fronds (G, group of 18), to minute plants (H, group of 22).

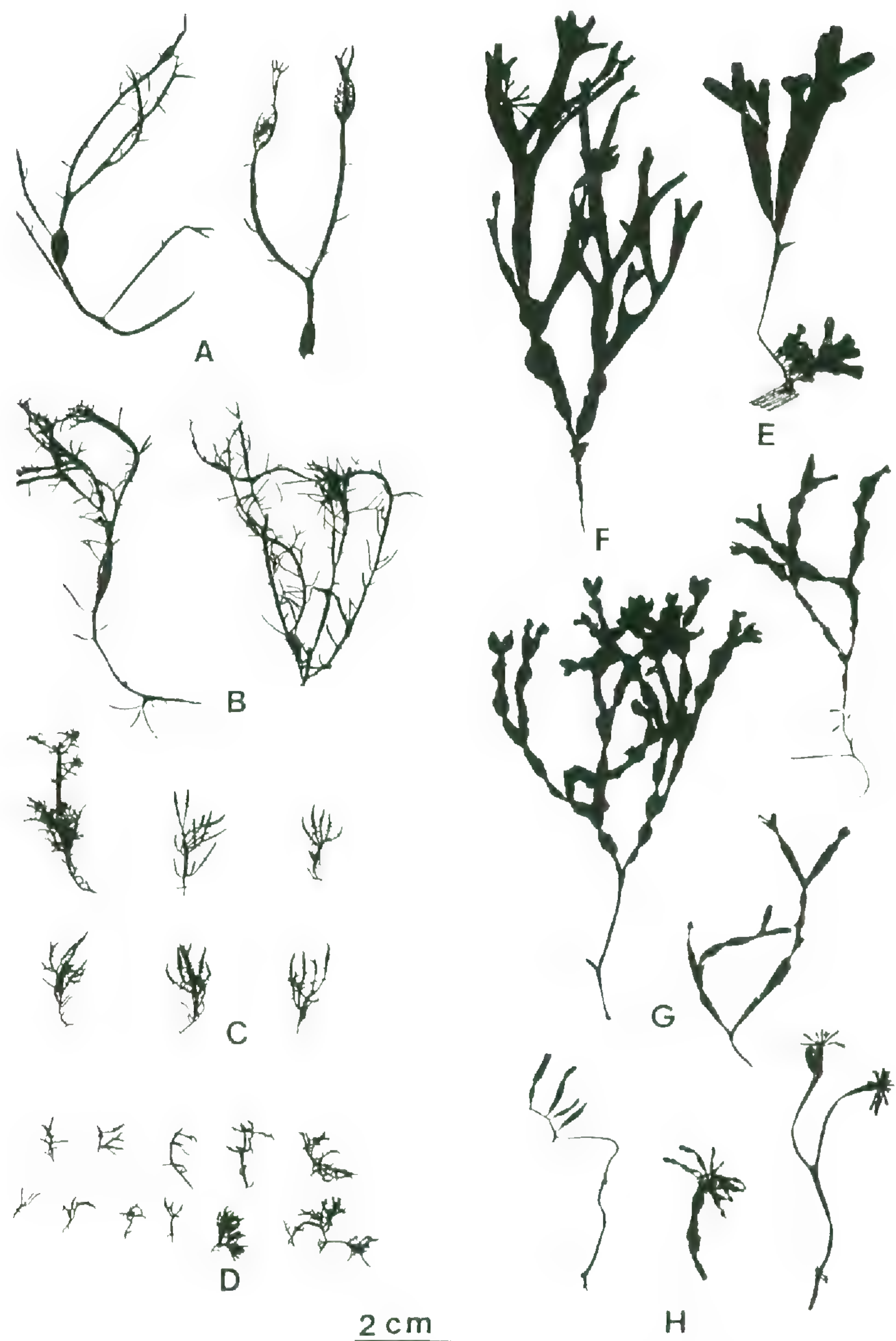


Figure 3. Silhouettes of morphological variability in two fucoid taxa from Brave Boat Harbor, Maine. Detached *Ascophyllum nodosum* grading from two large fragments (A), to a pair of more proliferous fragments (B), to progressively smaller fronds (C, group of 6), and finally to minute plants of the ecad *scorpioides* (D, group of 11). Attached (E) and detached fronds of *Fucus vesiculosus* (F) grading into *F. vesiculosus* ecad *volubilis* (G, group of 3), and then to more proliferous and smaller residual specimens (H, group of 3).

Table 2. Sediment characteristics of core samples (top 5 cm) from each of seven transect sites within Brave Boat Harbor's main tidal channel. The data represent percentages $\pm$ 1 SD of total values based on the means of duplicate cores.

Site #	Mean % total composition $\pm$ 1 SD						
	1	2	3	4	5	6	7
Distance inland (km)	0.29	0.31	0.38	0.40	0.79	0.86	1.12
Water content (%)	26.0 ± 0.9	30.0 ± 2.4	37.0 ± 1.2	36.0 ± 1.5	51.0 ± 2.3	54.0 ± 0.5	55.0 ± 0.7
Medium size particles (> 0.125 mm)	70.0 ± 8.1	55.0 ± 6.6	58.0 ± 8.8	58.0 ± 14.0	30.0 ± 7.4	32.0 ± 7.4	33.0 ± 3.1
Fine sand, silt parti- cles (< 0.063 mm)	3.0 ± 1.0	3.0 ± 1.3	4.0 ± 1.3	5.0 ± 1.3	10.0 ± 1.7	11.0 ± 2.5	11.0 ± 3.4

Thus, the terms low and high transplants refer to the resulting rather than the initial materials. Duplicate cores of each *in situ* population were taken in order to evaluate initial biomass and morphometric patterns (see below). The transplant samples were harvested after approximately one year (i.e., June 1999) and several morphometric features were compared with previous *in situ* materials (see above).

Replicate core samples at individual transect sites were pooled and the frond morphology of 25 plants assessed, including their length (cm), width (mm), weight (g), burial depth (mm) or the blackened zone due to anoxic conditions, numbers of branches and fertile tips, and numbers of marginal and surficial cryptostomata or hair pits (cf. Niell et al. 1980). Only flattened fronds of *Fucus* plants were assessed for cryptostomatal patterns, as the small cylindrical branches of the muscoides-like *Fucus* had few cryptostomata and could not be directly compared with other flattened taxa. Cryptostomatal ratios were assessed using a representative ocular field (100 $\times$). Ultimately, mean values and standard deviations for each of the above described morphometric parameters were calculated.

Sediment particle size and water content were determined at each of the seven transect sites (Table 2), using a stainless steel tube (11.3 cm²). Duplicate cores (10 cm long) were extracted at each site within dense populations of muscoides-like *Fucus* and placed in individually labeled plastic bags that were returned to the laboratory. Samples were either processed immediately or refrigerated at 10°C for later analysis. The above-ground plant ma-

terial was removed, including the attached and/or buried seaweed samples, and the cores were oven dried at 60°C for 48 hours. Percent water of each core was determined by weighing samples before and after drying, with the measurements having an accuracy of ± 0.01 g. Dried samples were sieved for particle size.

RESULTS

Ecology of muscoides-like *Fucus*. As shown in Table 2, surface sediments within BBH are sandy, with those in the outer to middle channel (0.29–0.40 km) having 55 to 70% medium-sized sand particles (> 0.125 mm diameter). By contrast, inner sites (0.79–1.12 km) show a decrease in coarse particles and an enhancement of very fine sand, clay, and silt (< 0.063 mm). The percentage of pore water showed a conspicuous increase from 0.29–1.12 km inland (Table 2). Hence, there was more extensive standing water and enhanced filamentous algae (i.e., one or more species of *Vaucheria* and *Rhizoclonium riparium*) at inner than outer sites (see below).

Nine seaweed taxa and seven flowering plant species were found on the seven transects (Table 1). The muscoides-like *Fucus*, *Rhizoclonium riparium*, and *Vaucheria* spp. were the most cosmopolitan seaweeds (100% occurrence), followed by *Ascophyllum nodosum* ecad *scorpioides* (85.7%), *F. spiralis* (85.7%), *Melanosiphon intestinalis* (D. A. Saunders) M. J. Wynne (57.1%), *A. nodosum* (28.6%), *F. vesiculosus* ecad *volubilis* (28.6%), and *F. spiralis* ecad *lutarius* (14.3%). The most ubiquitous flowering plants were *Spartina patens* (100% occurrence), *Limonium nashii* Small (85.7%), and *S. alterniflora* (85.7%), with rare occurrences of *Salicornia europaea* L., *Suaeda maritima* (L.) Dumort. and *Triglochin maritima* L. (14.3%). Overall, the mean number of taxa and the percentage occurrence of seaweeds on the various transects were 6.0 ± 0.57 taxa and $66.9 \pm 35.1\%$, respectively, versus 3.4 ± 1.3 taxa and $49.0 \pm 39.4\%$ for flowering plants (Table 1). Of the six furoid algae, two grew attached (*Ascophyllum nodosum* and *Fucus spiralis*), three occurred as entangled/buried plants (*A. nodosum* ecad *scorpioides*, *F. spiralis* ecad *lutarius*, and *F. vesiculosus* ecad *volubilis*), and one (the muscoides-like *Fucus*) formed embedded, turf-like masses. The filamentous green alga *Rhizoclonium riparium* produced extensive, entangled masses on muddy surfaces (see below), while the sediment-in-

habiting yellow-green algal genus *Vaucheria* often grew with it. The tubular brown alga *Melanosiphon intestinalis* grew on erosive, sandy cliffs at outer-middle sites. No attached populations of *F. vesiculosus* were found on any of the transects (see below).

Table 3 illustrates biomass patterns on two transect sites located at 0.40 km and 0.79 km inland. The outer transect was ~ 4.6 m long and had a gradual slope (~ 0.26 m vertical/1.0 m horizontal), while the inner one was shorter (~ 3.5 m) and had a steeper shoreline (~ 0.34 m vertical/1.0 m horizontal). In comparing biological patterns, the muscoides-like *Fucus* at the 0.40 km transect had a greater biomass, it extended higher vertically ($+3.0$ to $+3.4$ m), and was primarily associated with *Spartina patens*. By contrast, plants growing at the inner site exhibited a reduced biomass, a more circumscribed zonation (i.e., $+1.8$ to $+2.4$ m), and were usually associated with *S. alterniflora*. Although not illustrated, the plants' horizontal distribution (i.e., belt) on the seven transects also varied spatially, being 2.1 ± 1.8 m (0.90) between 0.29–4.0 km, 0.92 ± 0.174 m (0.3) at 0.79–1.12 km, and averaging overall 1.6 ± 1.5 m (1.2) for the seven sites. Thus, inner populations typically formed narrow belts adjacent to vertical bluffs, while they were more expansive towards the mouth.

As shown in Table 3, *Fucus spiralis* and *Melanosiphon intestinalis* were the most abundant seaweeds on the outer transect and were either reduced or absent at the inner site. *Ascophyllum nodosum* ecad *scorpioides*, *Spartina alterniflora*, and *S. patens* all showed the opposite pattern, being more abundant at inner than outer sites. *Spartina patens* also occurred at lower elevations at 0.40 km ($\sim +1.6$ to $+2.4$ m) than 0.79 km inland ($\sim +3.1$ m). *Fucus vesiculosus* ecad *volubilis* was only found within the low intertidal at 0.79 km. *Fucus spiralis* and the muscoides-like *Fucus* populations exhibited contrasting vertical distributions at the outer site, with the former dominating the lower and the latter the upper shoreline.

Figure 4 illustrates spatial biomass patterns for six fucoid taxa, with the data being expressed as mean biomass values (i.e., g dry wt./m²) per transect. Populations of the muscoides-like *Fucus* (Figure 4A) were maximal (286.0 ± 24.7 to 389.0 ± 420.0 g dry wt./m²) at the three outer sandy sites (i.e., 0.29–0.38 km, Table 1), while they varied from 28.0 ± 8.5 to 208.0 ± 141.4 g dry wt./m² at the inner more silty sites (i.e., 0.79–1.12 km, Table 1). *Fucus spiralis* exhibited its maximum and minimum biomass

Table 3. Biomass patterns versus height above mean low water (MLW) for dominant intertidal plants at two transect sites within Brave Boat Harbor's main tidal channel. Symbols: ANS = *Ascophyllum nodosum* ecad *scorpioides*, FMUSC = muscoides-like *Fucus*, FS = *F. spiralis*, FVV = *F. vesiculosus* ecad *volubilis*, MI = *Melanosiphon intestinalis*, SA = *Spartina alterniflora*, and SP = *S. patens*.

Height above MLW (m)	Biomass (g dry wt./m ² ± 1 SD)						
	ANS	FMUSC	FS	FVV	MI	SA	SP
INNER TRANSECT (0.40 km)							
+2.2	0	0	627.0 ± 23.0	0	278.0 ± 7.0	12.0 ± 6.0	0
+2.4	0	0	145.0 ± 33.0	0	379.0 ± 130.0	16.0 ± 2.0	0
+2.8	0	0	144.0 ± 105.0	0	314.0 ± 136.0	0	0
+3.0	65.0 ± 39.0	82.0 ± 44.0	289.0 ± 7.0	0	0	0	691.0 ± 680.0
+3.2	12.0 ± 2.0	170.0 ± 21.0	44.0 ± 31.0	0	0	27.0 ± 27.0	367.0 ± 114.0
+3.4	4.0 ± 4.0	258.0 ± 111.0	16.0 ± 16.0	0	0	241.0 ± 100.0	1387.0 ± 522.0
OUTER TRANSECT (0.79 km)							
+1.6	2998.0 ± 173.0	0	0	1941.0 ± 768.0	0	1333.0 ± 242.0	0
+1.8	168.0 ± 87.0	34.0 ± 15.0	18.0 ± 18.0	0	0	0	0
+2.2	7688.0 ± 421.0	0	0	190.0 ± 112.0	0	777.0 ± 100.0	0
+2.4	37.0 ± 5.0	22.0 ± 11.0	0	0	0	405.0 ± 179.0	1985.0 ± 559.0
+2.6	0	0	0	0	0	111.0 ± 14.0	4126.0 ± 713.0
+2.8	0	0	0	0	0	0	0

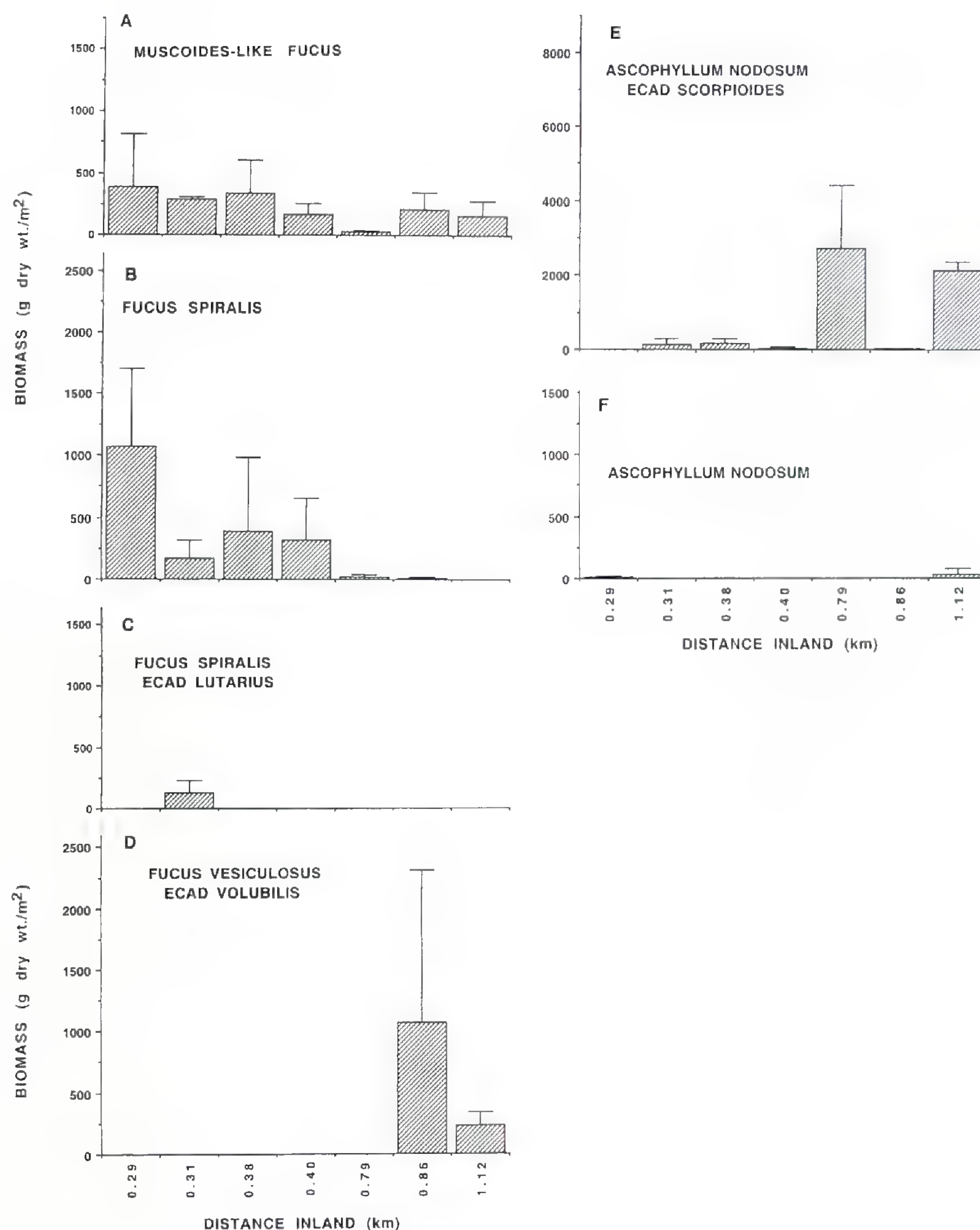


Figure 4. Mean biomass patterns (g dry wt./m² ± 1 SD) for muscoides-like *Fucus* (A), *F. spiralis* (B), *F. spiralis* ecad *lutarius* (C), *F. vesiculosus* ecad *volubilis* (D), *Ascophyllum nodosum* ecad *scorpioides* (E), and *A. nodosum* populations (F) on seven transects within Brave Boat Harbor's main tidal channel, with the sites ranging from 0.29–1.12 km inland.

(Figure 4B) at 0.29 km (1072.5 ± 632.9 g dry wt./m²) and 0.86 km (8.5 ± 12.0 g dry wt./m²), respectively. The three entangled fucoid ecads *F. spiralis* ecad *lutarius*, *F. vesiculosus* ecad *volubilis* and *Ascophyllum nodosum* ecad *scorpioides* exhibited contrasting distributional patterns (Figures 4C–E). *Fucus spiralis*

ecad *lutarius* was only found at the 0.31 km site (130.0 ± 94.8 g dry wt./m²), while *F. vesiculosus* ecad *volubilis* was present at 0.86 km (1065.6 ± 1238.1 g dry wt./m²) and 1.12 km inland (230.0 ± 111.7 g dry wt./m²). The mean biomass for *A. nodosum* ecad *scorpioides* varied from 0 to 2722.0 ± 1704.5 g dry wt./m² (Figure 4E), with the highest values occurring at inner silty sites (i.e., 0.79 and 1.12 km). Attached populations of *A. nodosum* were uncommon (10.0 ± 13.4 to 31.0 ± 43.8 g dry wt./m²) and only occurred at the outer- and innermost sites.

The overall mean biomass patterns for various seaweeds and flowering plants on the seven transects are summarized in Table 1. Of the six furoid algae, *Ascophyllum nodosum* ecad *scorpioides* was the dominant taxon, followed by *Fucus vesiculosus* ecad *volubilis*, *F. spiralis*, the muscoides-like *Fucus*, *F. spiralis* ecad *lutarius*, and *A. nodosum*. Overall, *A. nodosum* ecad *scorpioides* was the dominant species (868.2 ± 1225.0 g dry wt./m²), while *A. nodosum* was the least abundant (20.5 ± 14.8 g dry wt./m²); the muscoides-like *Fucus* exhibited an intermediate pattern (226.3 ± 122.3 g dry wt./m²) relative to the other taxa. Regarding the flowering plants, the mean biomass was 982.8 ± 1836.9 g dry wt./m² with this varying from 28.0 ± 38.9 (*Salicornia europaea*) to 5095.7 ± 4159.2 g dry wt./m² (*Festuca rubra*). Thus, the mean number and percent occurrence of seaweed taxa per site were higher than for flowering plants, while the biomass values for flowering plants exceeded that of the seaweeds.

As shown in Table 1, the muscoides-like *Fucus* exhibited varying affinities with the other five furoid taxa. Thus, it occurred at 6 of the 7 sites where *F. spiralis* and *Ascophyllum nodosum* ecad *scorpioides* were found (85.7% similarity), while it exhibited a reduced affinity with *A. nodosum* (28.6%), *F. vesiculosus* ecad *volubilis* (28.6%), and *F. spiralis* ecad *lutarius* (14.3%). The muscoides-like *Fucus* was also consistently found in association with the sediment-inhabiting *Vaucheria* spp.–*Rhizoclonium riparium* complex, plus the flowering plant *Spartina patens* (100% similarity). *Limonium nashii* and *S. alterniflora* also showed a strong affinity to the muscoides-like *Fucus*, with populations occurring together at six of the seven sites (i.e., 85.7% similarity). Based on the above information the following comments can be made: (1) the muscoides-like *Fucus*, *F. spiralis*, and *A. nodosum* ecad *scorpioides* exhibited very similar distributional patterns, albeit the muscoides-like plants and *A. nodosum* ecad *scorpioides* had

contrasting ecological requirements (cf. Table 2; Figure 4A, E); (2) attached *in situ* *A. nodosum* and *F. spiralis* and their corresponding detached ecads (i.e., *A. nodosum* ecad *scorpioides* and *F. spiralis* ecad *lutarius*) also had different ecological requirements (cf. Figure 4B, C, E, F); (3) *F. vesiculosus* was only represented on the transects by its ecad *volubilis*, with a few attached and scattered populations occurring within the main tidal channel and adjacent open coast (Mathieson et al. 2001); and (4) the muscoides-like *Fucus* was typically found beneath the canopy of sparse *Spartina patens*, often growing in association with the *Vaucheria* spp.–*Rhizoclonium riparium* complex.

Fucoid morphology. Figure 5 presents six morphological features for the muscoides-like populations at seven sites within BBH, expressed as mean values $\pm$ SD per site. Few obvious patterns were evident, except for a diminishment of burial depths from the outermost site inland (Figure 5D) and a dominance of marginal versus surficial pits (Figure 5F). Overall, frond length (Figure 5A) varied from 11.2–16.1 mm (mean = 13.2 ± 4.2 mm), width (Figure 5B) from 0.9–1.4 mm (mean = 1.1 ± 0.2 mm), weight (Figure 5C) from 0.1–0.17 g (mean = 0.1 ± 0.03 g), burial depth (Figure 5D) from 3.1–8.3 (mean = 5.6 ± 1.8 mm), number of branches per frond (Figure 5E) from 3.4–6.9 (mean = 4.6 ± 1.1), and numbers of marginal and surface pits (Figure 5F) from 1.0–15.8 (mean = 8.1) and 0.0–1.65 (mean = 0.74), respectively. Overall, the mean ratio of marginal to surface pits was 11:1.

Figure 6 summarizes horizontal and vertical differences in stature and morphology for two populations of the muscoides-like *Fucus* (0.29 and 0.40 km), expressed as mean values $\pm$ SD. Typically plants from lower elevations were longer than those from upper ones (Figure 6A), with the smallest plants (14.4 ± 4.3 mm) occurring at the outer, upper site and the largest at the lower, inner location (28.9 ± 12.1 mm). Frond width and weight (Figure 6B, C) were widest and heaviest at lower elevations. Burial depth (Figure 6D) was more circumscribed at outer (6.6–6.8 mm) than inner (8.7–12.9 mm) sites. The high numbers of branches per frond (Figure 6E) at the lower, inner site (17.9 ± 26.1) are indicative of extensive proliferations (cf. Figure 2F), with the other three samples having limited proliferations and lower numbers of branches per frond (i.e., 7.2–12.5). Fronds of the muscoides-like

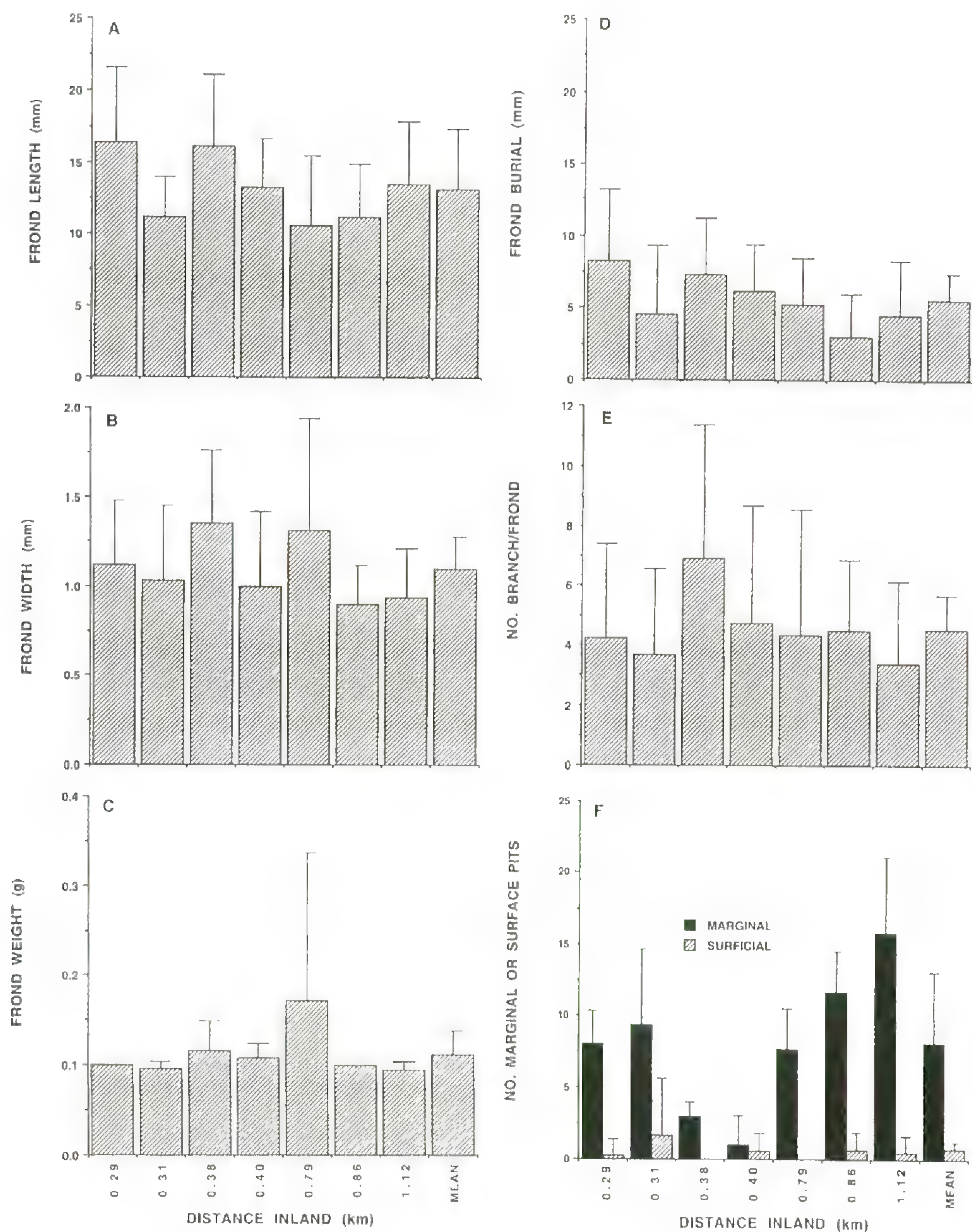


Figure 5. A synopsis of six morphological features (± 1 SD) for muscoides-like *Fucus* populations at seven locations within Brave Boat Harbor's main tidal channel (0.29–1.12 km inland), expressed as mean site values ($\pm$ SD) for frond length (A), frond width (B), frond weight (C), burial depth (D), number of branches per frond (E), and number of marginal and surficial pits (F); the overall mean values for each parameter are also shown.

Fucus were dominated by marginal pits (Figure 6F), with the occurrence of surficial pits being inconsistent and reduced in numbers.

Figure 7 demonstrates morphological features for seven *Fucus spiralis* populations within BBH, expressed as mean values $\pm$ SD

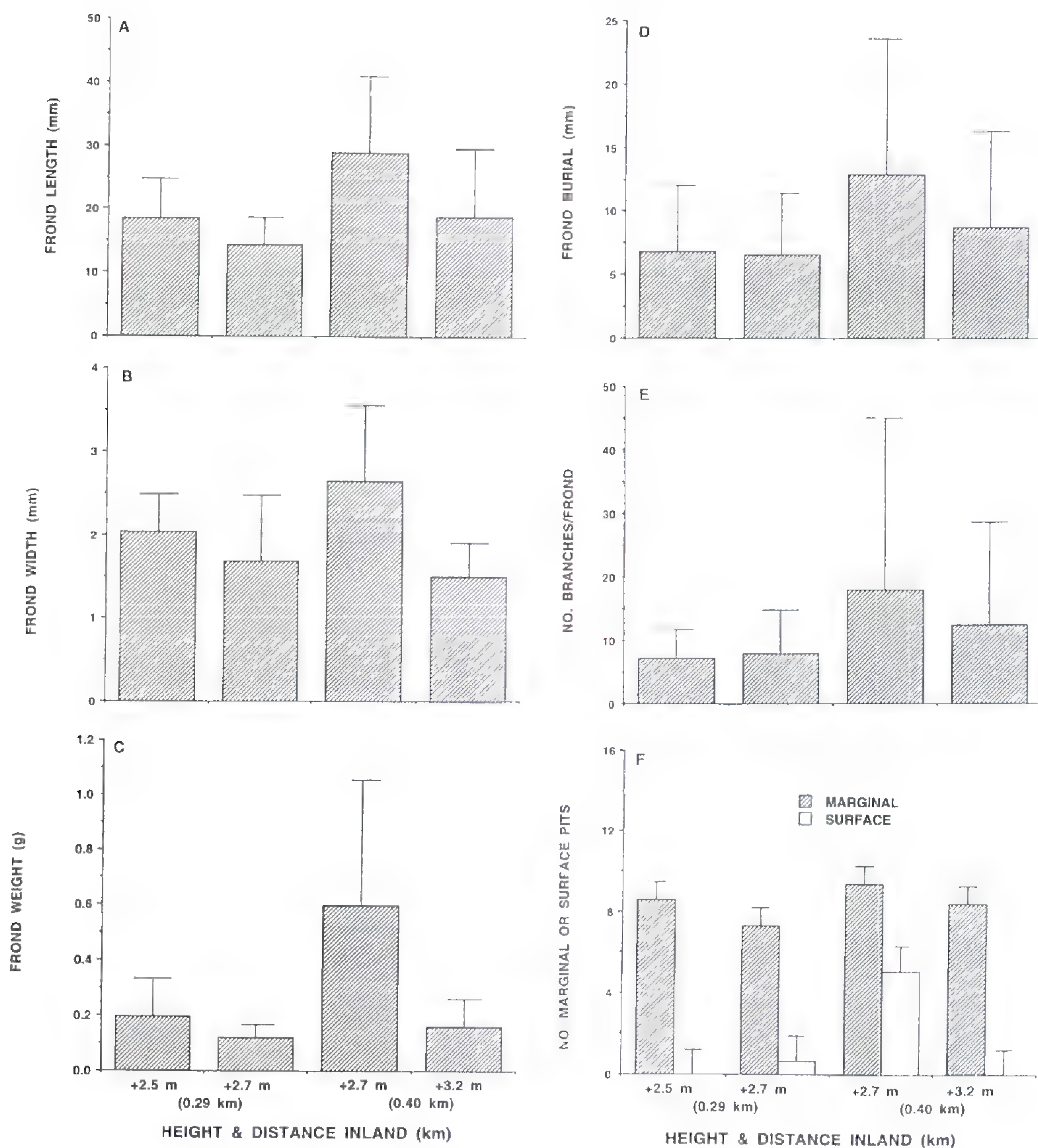


Figure 6. A synopsis of six morphological features (± 1 SD) for Brave Boat Harbor muscoides-like *Fucus* at two sites (0.29 and 0.40 km inland) and multiple elevations (+2.5 and +2.7 m versus +2.7 and +3.2 m), with the values being expressed as mean frond length (A), width (B), weight (C), burial depth (D), number of branches per frond (E), and number of marginal and surficial pits (F).

per site. The smallest, narrowest, and lightest fronds occurred at the innermost estuarine site (0.79 km) where the species occurred (18.5 ± 3.5 mm, 3.3 ± 0.4 mm, and 0.6 ± 0.01 g, respectively; Figure 7A–C). Analogous patterns occurred for the numbers of branches per frond and reproductive tips (Figure 7D, E). By contrast, these same parameters were relatively uniform (e.g., length and width), decreased clinally (weight), or were quite variable at outer-middle sites (e.g., # of branches and fertile tips). Fronds of

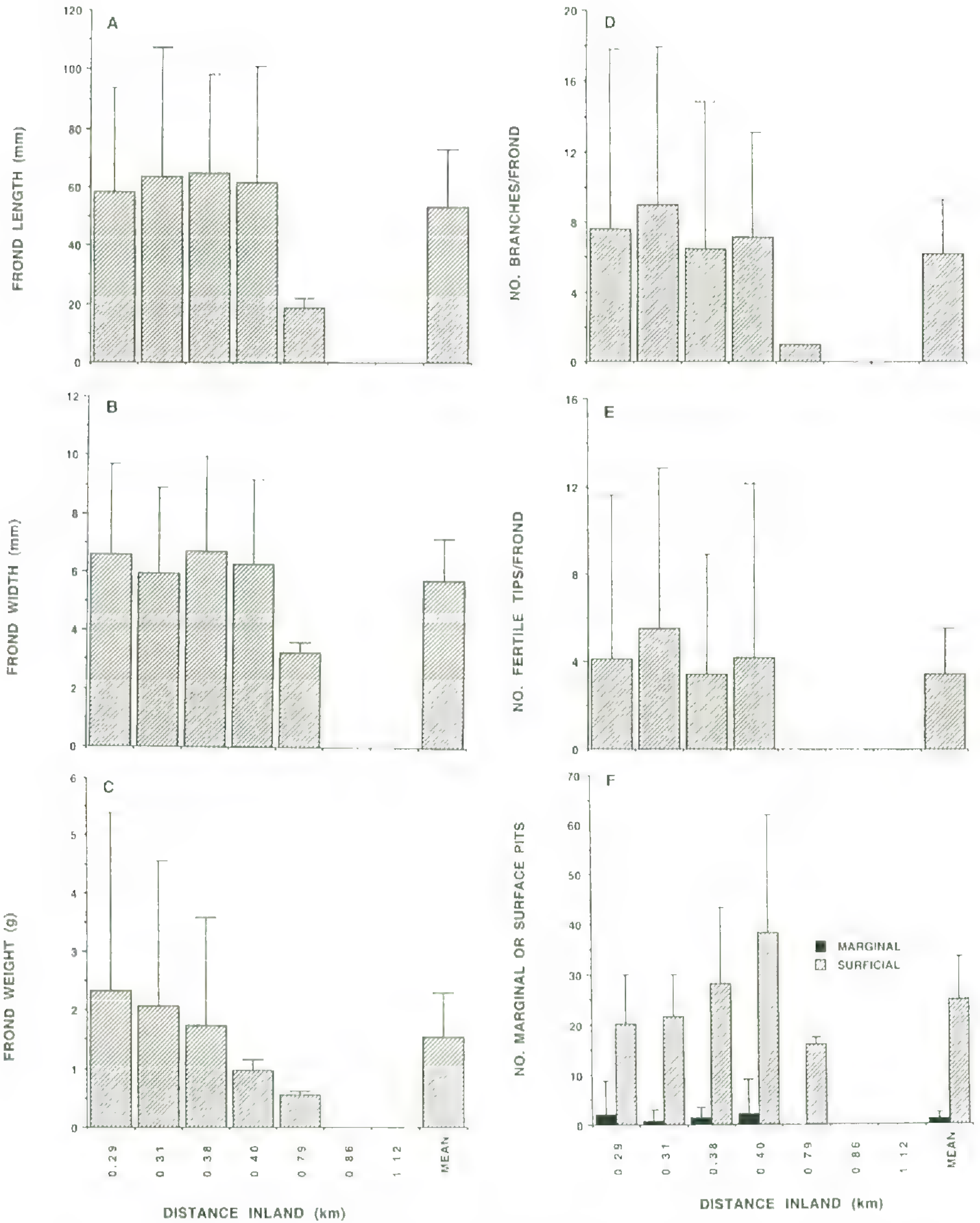


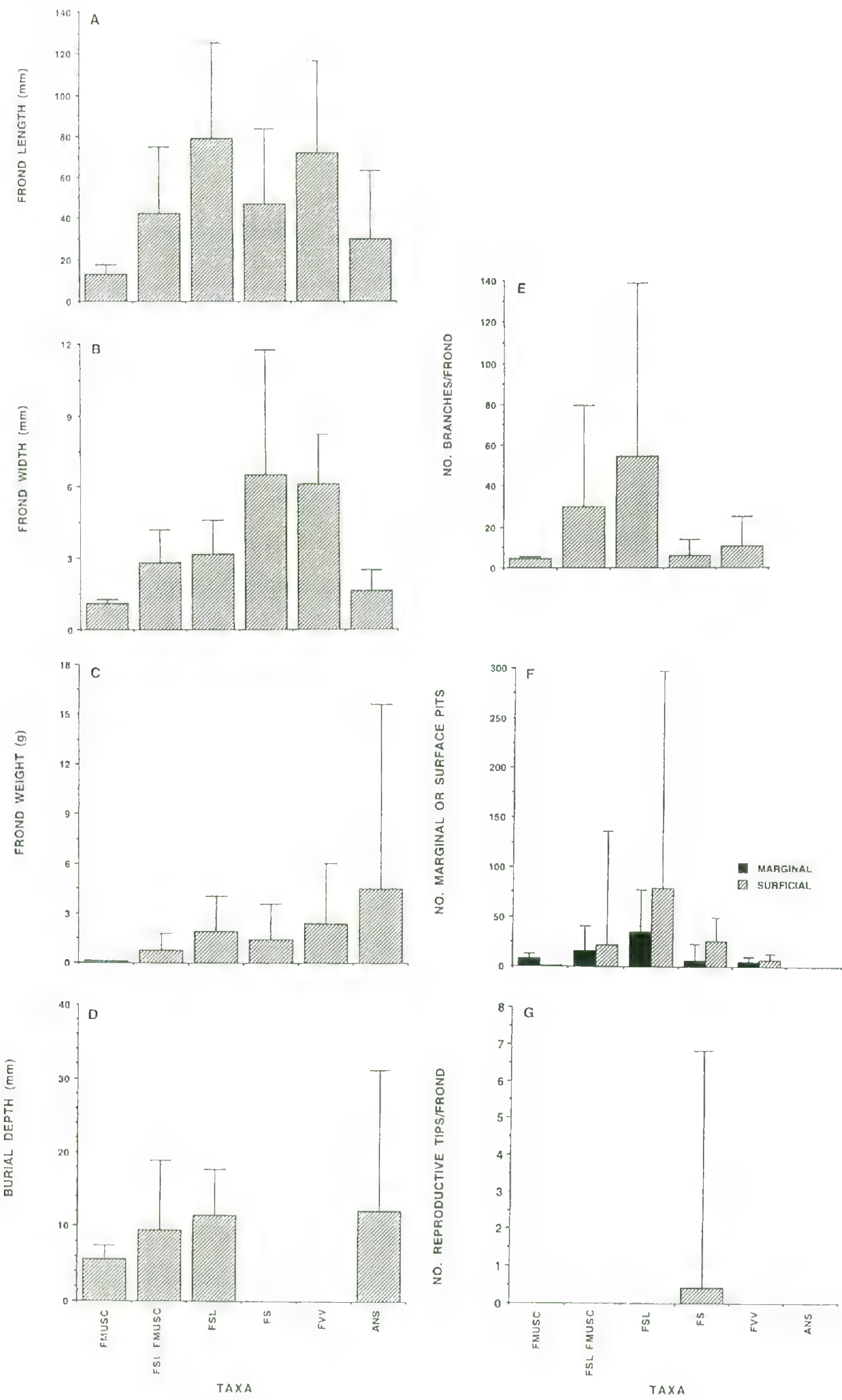
Figure 7. A synopsis of six morphological features (± 1 SD) for *Fucus spiralis* populations at seven locations within Brave Boat Harbor's main tidal channel (0.29–0.86 km inland), expressed as mean site values ($\pm$ SD) for frond length (A), width (B), weight (C), number of branches per frond (D); number of fertile tips per frond (E); and number of marginal and surficial pits (F); the overall means ($\pm$ SD) for each parameter are also shown.

F. spiralis had fewer marginal (0.0–2.2, mean = 1.3 ± 0.9) than surficial pits (16.0–38.2, mean = 24.8 ± 8.6), which contrasts with the situation in the muscoides-like *Fucus* (cf. Figures 5F, 7F). The overall mean values for *F. spiralis* fronds were $53.4 \pm$

19.7 mm long, 5.8 ± 1.4 mm wide, 1.5 ± 0.8 g damp-dried weight, 6.3 ± 3.1 number of branches, 3.5 ± 2.1 fertile tips per frond, and an overall mean ratio of marginal to surficial pits of 1:19.

Figure 8 compares the primary morphological features of six BBH fucoid taxa and complexes, including the muscoides-like *Fucus* (FMUSC), fragmented *F. spiralis* ecad *lutarius* grading into the muscoides-like plants (i.e., FSL–FMUSC), *F. spiralis* ecad *lutarius*, *F. spiralis*, *F. vesiculosus* ecad *volubilis*, and *Ascophyllum nodosum* ecad *scorpioides*. Frond length, width, weight, and burial depth were smallest in the muscoides-like *Fucus* (Figure 8A–D), averaging 13.2 ± 4.2 mm, 1.1 ± 0.2 mm, 0.11 ± 0.03 g, and 5.6 ± 1.8 mm, respectively. The other five plants showed variable patterns, with frond lengths ranging from 29.9 ± 33.4 mm (*A. nodosum* ecad *scorpioides*) to 78.8 ± 46.4 mm (*F. spiralis* ecad *lutarius*), widths from 1.6 ± 0.8 mm (*A. nodosum* ecad *scorpioides*) to 6.5 ± 5.2 mm (*F. spiralis*), weights from 0.8 ± 1.0 g (FSL–FMUSC) to 4.5 ± 11.2 g (*A. nodosum* ecad *scorpioides*), and burial depths from 9.6 ± 9.4 mm (FSL–FMUSC) to 12.2 ± 19.0 mm (*A. nodosum* ecad *scorpioides*). The number of branches per frond for the five fucoids (Figure 8E) ranged from 6.2 ± 7.5 (*F. spiralis*) to 54.7 ± 84.0 (*F. spiralis* ecad *lutarius*), with the muscoides-like *Fucus* being 4.6 ± 1.1 . Hair pits (Figure 8F) were absent in *A. nodosum* ecad *scorpioides*; the muscoides-like *Fucus* primarily had marginal pits (8.10:0.74 or 11:1, marginal to surficial), while the other four had a prevalence of surficial pits: FSL–FMUSC (16.3:22.2 or 1:1.4), *F. spiralis* ecad *lutarius* (34.3:79.4 or 1:2.3), *F. spiralis* (1.3:24.8 or 1:19), and *F. vesiculosus* ecad *volubilis* (4.7:7.0 or 1:1.5). Reproductive tips (i.e., receptacles) only occurred on *F. spiralis* (0.4 ± 6.4), with these showing a wide range of values (Figure 8G). In summary, the muscoides-like *Fucus* stature (i.e., length, width, and weight) was consistently smaller than the other five fucoid taxa and complexes, while it also had a greater dominance of marginal than surficial pits.

A wide range in morphology is evident in the silhouettes of the three fucoid populations shown in Figure 2. *Fucus spiralis* ranges from young flattened germlings (Figure 2A), to reproductively mature and flattened fronds (Figure 2B), to terete residual and proliferous specimens (Figure 2C). Detached specimens of *F. spiralis* ecad *lutarius* grade from large, fragmented fronds



(Figure 2D), to proliferous and small plants (Figure 2E). The turf-like specimens of the muscoides-like *Fucus* vary from tufted, elongated specimens (Figure 2F), to short, individual fronds (Figure 2G), to minute plants (Figure 2H). Overall, a morphological continuum is evident between attached/proliferous *F. spiralis*, detached/entangled *F. spiralis* ecad *lutarius*, and the muscoides-like *Fucus* (Figure 2A–H); the transition is associated with a diminution of stature, enhanced proliferation, degeneration of residual fronds, and extensive dichotomic splitting (*sensu* Hartog 1972) as noted below.

Analogous morphological variability occurs in *Ascophyllum nodosum* ecad *scorpioides*, with initial detached and slightly proliferous fragments (Figure 3A) becoming highly proliferous (Figure 3B) and these in turn becoming progressively smaller and more residual (Figure 3C, D). The smallest material of *A. nodosum* ecad *scorpioides* is reminiscent of muscoides-like *Fucus* (cf. Figures 2G, 2H, 3D), except that it lacks hair pits (Figure 8F) and is more irregularly branched. Morphological variability in *F. vesiculosus* also ranges from attached and detached fronds (Figure 3E, F), to spiraled fragments of *F. vesiculosus* ecad *volubilis* (Figure 3G), to smaller, residual, and proliferous specimens (Figure 3H). Thus, the pattern of fragmentation, enhanced proliferation, and degeneration of residual fronds within *A. nodosum* ecad *scorpioides* and *F. vesiculosus* ecad *volubilis* is analogous to that previously described (Figure 2). Even so, the smallest fronds of *F. vesiculosus* ecad *volubilis* in BBH (Figure 3H) were always larger than those of the muscoides-like *Fucus* and *A. nodosum* ecad *scorpioides* (Figure 2G, H, 3D).

Transplant studies. Reciprocal transplants of fucoids between +2.0 and +3.4 m above MLW at the 0.40 km BBH site resulted in pronounced morphological changes (Figure 9). Four

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Figure 8. Six morphological features (± 1 SD) of muscoides-like *Fucus* (FMUSC), *F. spiralis* ecad *lutarius* grading into muscoides-like plants (FSL–FMUSC), *F. spiralis* ecad *lutarius* (FSL), *F. spiralis* (FS), *F. vesiculosus* ecad *volubilis* (FVV), and *Ascophyllum nodosum* ecad *scorpioides* (ANS), with the data being expressed as mean frond length (A), width (B), weight (C), burial depth (D), number of branches per frond (E), number of marginal and surficial pits (F), and number of reproductive tips per frond (G).

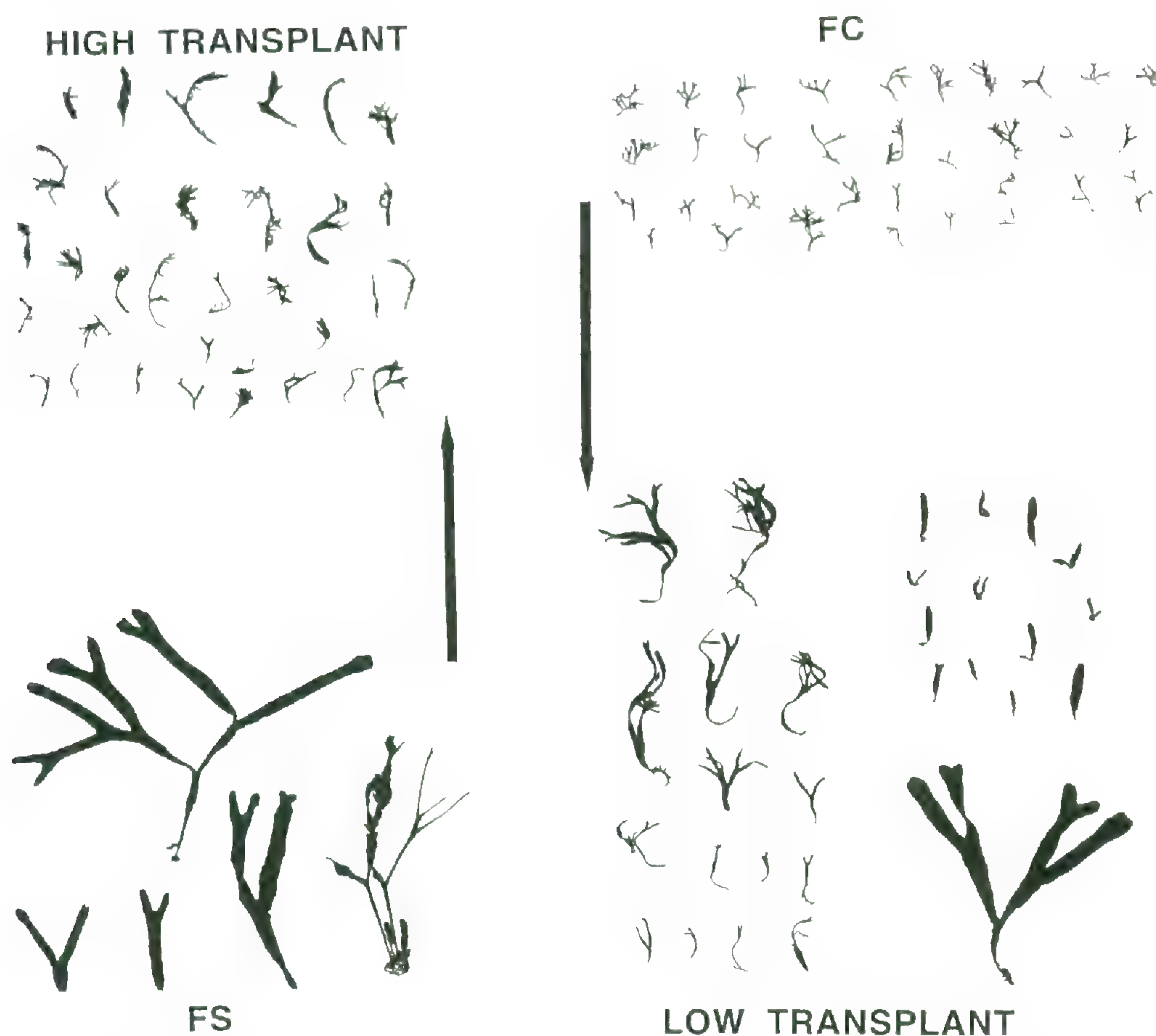


Figure 9. Silhouettes of fucoid plants associated with a reciprocal transplant experiment at a site 0.38 km inland within Brave Boat Harbor's main tidal channel. The results of a transfer of *in situ* *Fucus spiralis* (FS) from the low to high intertidal zone (HIGH TRANSPLANT) are shown in the bottom and top left sides respectively (up arrow). The results of the opposite transfer of *in situ* muscoides-like plants (FMUSC) to the low intertidal (LOW TRANSPLANT) are shown in the upper and lower right sides, respectively (down arrow).

populations were assessed: low *in situ* *Fucus spiralis*, high *in situ* muscoides-like *Fucus*, low transplants of muscoides-like *Fucus*, and high transplants of *F. spiralis*. Low *in situ* *F. spiralis* are longer, wider, and have a greater number of branches and reproductive tips than high *in situ* muscoides-like plants (Figure 10A–C). An analogous pattern was evident when comparing the former plants and the resulting high transplant mixture of *F. spiralis* *ecad lutarius* and muscoides-like plants (i.e., FSL–FMUSC), which was very fragmented, proliferous, and totally vegetative (Figures 2D–E and 9).

In comparing high *in situ* muscoides-like plants with the re-

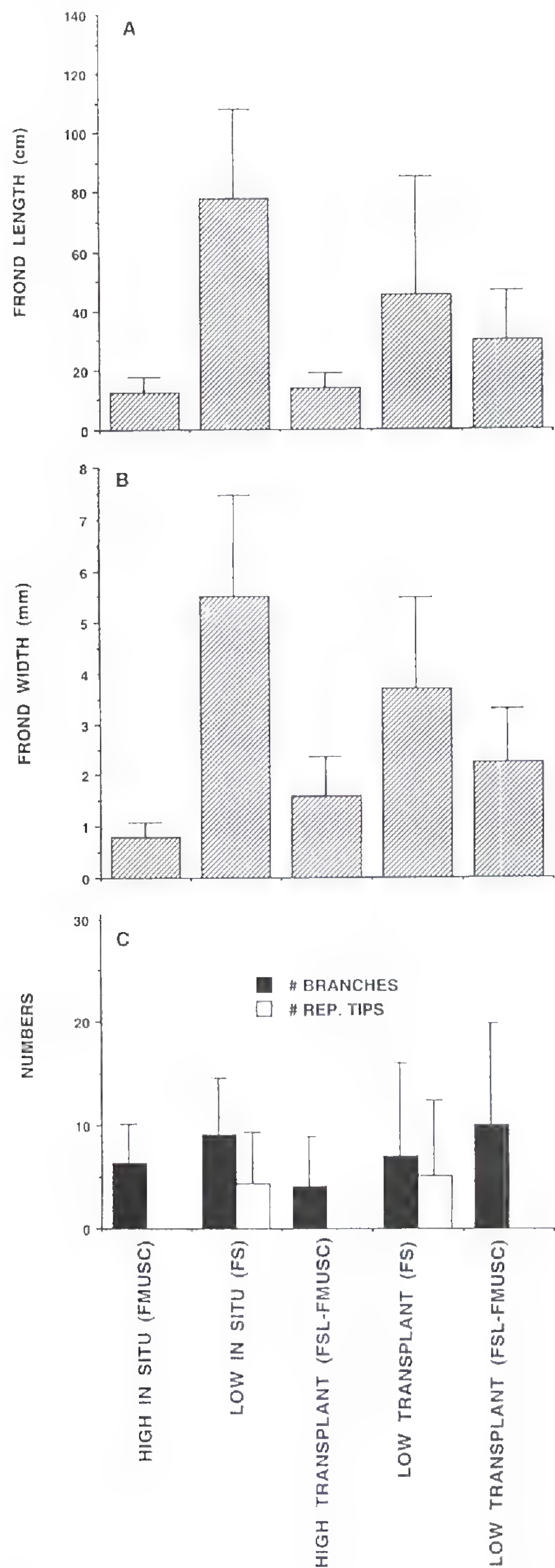


Figure 10. Morphological comparisons (± 1 SD) of five fucoid populations associated with a reciprocal transplant experiment at a site 0.38 km inland within Brave Boat Harbor's main tidal channel. Measurements include mean frond length (A) and width (B), plus the numbers of branches and reproductive tips (C). The plants include *in situ* muscoides-like *Fucus*

sulting low transplants (Figures 9 and 10), four major patterns were evident: (1) low transplants were heterogenous, consisting of newly colonized and reproductive *Fucus spiralis*, plus proliferous and fragmented FSL–FMUSC; (2) frond lengths and widths of all transplants were conspicuously greater; (3) the numbers of branches within high *in situ* muscoides-like plants were somewhat reduced versus low transplants of FSL–FMUSC; and (4) reproductive structures were found only on low transplants of *F. spiralis*. The main morphological responses of high transplants were enhanced fragmentation, stunting, proliferation, and reduced reproduction. By contrast, low transplants produced heterogenous material (i.e., FSL–FMUSC and newly colonized *F. spiralis*), and had enhanced frond length and circumscribed reproduction (i.e., only *F. spiralis* was fertile).

DISCUSSION

Our results indicate that the dwarf muscoides-like *Fucus* plants from BBH are phenotypic variants (i.e., ecads) of *F. spiralis*; thus they have a different origin than similar growth forms in Europe originally designated as *F. vesiculosus* var. (ecad) *muscoides* (cf. Baker and Bohling 1916; Cotton 1912; Niell et al., 1980) and now regarded as *F. cottonii* (Wynne and Magne 1991). The dwarf muscoides-like *Fucus* plants have only recently been reported from the Northwest Atlantic (Sears 1998; South and Tittley 1986), with these records being based upon upper salt marsh collections from BBH that were found growing amongst *Spartina patens* (Mathieson et al. 2001). Cotton (1912), who designated a similar plant as *F. vesiculosus* var. *muscoides*, described it as a “remarkable dwarf *Fucus*” that grew on peaty salt marshes above the mean high-tide level at Clare Island, Ireland. He further noted that it was most common in the “best-drained areas” where it formed a “dense mossy turf” amongst several halophytes, being 5–6 cm long, 1–3 mm wide, and “very erect.” While working

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(FMUSC), *in situ* *F. spiralis* (FS), plus resulting plants of *F. spiralis* ecad *lutarius*–muscoides-like *Fucus* (HIGH TRANSPLANT FSL–FMUSC), *F. spiralis* (LOW TRANSPLANT FS), and *F. spiralis* ecad *lutarius*–muscoides-like *Fucus* (LOW TRANSPLANT FSL–FMUSC).

in several marshes in Scotland, Baker and Bohling (1916) recorded a similar dwarf plant, designating it *F. vesiculosus* ecad *muscoides*; they noted that it grew “on firm peaty salt marshes as a dense mossy turf.” Lynn (1935) also described a “thick mossy growth” of dwarf plants from Strangford Lough, Ireland, while Wynne and Magne (1991) cited similar features in recognizing this as a distinct species, *F. cottonii*.

In comparing the BBH muscoides-like *Fucus* plants with those from Europe (England, Wales, Scotland, Ireland, and Spain), the New England plants are much smaller (mean = 1.3 ± 0.4 cm long), they primarily occur in the high salt marsh amongst sparse *Spartina patens*, and are only occasionally associated with *Limonium nashii* and *S. alterniflora*. In BBH the plants appear as brown to black branching masses that are embedded (mean depth = 0.6 ± 0.2 cm) within coarse, sandy sediments. Their biomass and horizontal and vertical ranges become more circumscribed with increasing distance inland (Table 3). Regardless of elevation, the muscoides-like *Fucus* primarily grows as an understory plant, mostly within the high marsh. Further inland within BBH estuary (e.g., beyond 0.79 km) the plant is primarily restricted to a narrow band and may be associated with *S. alterniflora*. Typically, the muscoides-like *Fucus* is found on the edges of exposed high marshes in sandy well-drained sediments that exhibit extensive erosion. Using these ecological features we have subsequently located the plant at more than twenty New England salt marshes, ranging from northern Maine to Massachusetts (Mathieson and Dawes, unpubl. data).

Although the dwarf, moss-like fucoid populations recorded for Europe (Baker and Bohling 1916; Cotton, 1912; Lynn 1935; Niell et al. 1980; Wynne and Magne 1991) are probably derived from different species than those found in BBH (Mathieson et al. 2001), they have similar niche characteristics: (1) upper marshes (e.g., the *Spartina patens* zone) that are flooded only by spring tides; (2) regions with reduced water motion; and (3) a substratum that consists of firm, well-drained sediments. Baker and Bohling (1916) speculated that their dwarf habit was associated with low nutrient availability and acidic sediments. However, the well-drained sandy sediments in BBH (see above) suggest that acidity is an unlikely factor, while desiccation and reduced nutrients may be more critical. Our muscoides-like *Fucus* doesn't occur beneath *S. patens* when standing water is evident at low tide, with this

habitat typifying inner, poorly drained marsh. Further, it is uncommon where abundant growths of filamentous algae (e.g., *Rhizoclonium riparium* and *Vaucheria* spp.) grow beneath *S. patens*.

Based upon a variety of morphological observations and the results of our transplant studies we believe that the muscoides-like populations from BBH originate from *Fucus spiralis* via its detached/entangled ecad *lutarius* (Figures 2 and 9). Thus, there is an obvious morphological continuum and spatial proximity between *F. spiralis*, *F. spiralis* ecad *lutarius*, and the muscoides-like *Fucus* (Figure 2A–H), with fragments of *F. spiralis* ecad *lutarius* often occurring embedded near or within dense clumps of dwarf plants. Further, only scattered and inconspicuous populations of *F. vesiculosus* occurred within BBH (see above), while *F. vesiculosus* ecad *volubilis* was only recorded at the 0.86 and 1.12 km transects (Table 1). Transplant specimens exhibited an analogous morphological continuum between the two extreme morphologies (i.e., the muscoides-like *Fucus* and *F. spiralis*) via *F. spiralis* ecad *lutarius* (Figures 2 and 9). Thus, the transplant studies showed the origin of muscoides-like *Fucus* via degeneration and dichotomous splitting (*sensu* Hartog 1972) of *F. spiralis* ecad *lutarius*. The latter process is associated with incremental deposition of sediment, followed by basal frond decay that reaches a dichotomy, effectively separating the frond into two plants (Norton and Mathieson 1983). Our findings differ from Baker and Bohling (1916) and Niell et al. (1980) who proposed a connection between muscoides-like material and *F. vesiculosus*, with the latter paper documenting a morphological continuum between the two plants, the absence of *F. spiralis*, and the presence of only *F. vesiculosus* populations—the opposite of our findings in BBH!

In summary, we believe that the muscoides-like *Fucus* plants from BBH are part of a megaecad (*sensu* Clements 1905) associated with *F. spiralis*. The dwarf form develops within a unique and restrictive habitat, depending upon the availability and type of attached (parental) material. Thus, it appears that a muscoides-like morphology in both Europe and New England can be derived from more than one species (see above). The development of muscoides-like plants from BBH specimens of *F. spiralis* supports Naylor's (1936) observations that the latter species may produce small embedded marsh forms. Analogous patterns of fragmentation, proliferation, degeneration, and dwarfing have also been reported for *Ascophyllum nodosum* ecad *scorpioides* (Lynn

1935), plus the variety *coralloides* Baker and the ecads *libera* Baker (Baker and Bohling 1916) and *muscoides* Skrine of *Pelvetia canaliculata* (L.) Decaisne *et* Thuret (Baker 1912; Carter 1933; Skrine 1929). In describing such fucoids, Naylor (1936) points out that prevailing environmental conditions in salt marshes have tended to produce identical thalli in different species, which are almost indistinguishable in their vegetative state. For example, Carter's (1933) illustration of *P. canaliculata* ecad *muscoides* (Figure 26-1) and those of Wynne and Magne (1991) for *Fucus cottonii* (cf. Figure 1) are very reminiscent of the muscoides-like *Fucus* we have observed from BBH (cf. Figure 2G–H). Further, the small residual materials of *A. nodosum* ecad *scorpioides* from BBH are often difficult to distinguish from muscoides-like plants, except for the absence of hair pits and the more irregular branching (Figures 2G–H, 3D and 8F).

In discussing fucoid taxonomy, Fritsch (1945) has stated that there is considerable confusion regarding the taxonomy of detached/entangled plants like “*Fucus lutarius* Kützinger,” with some designating them as *F. vesiculosus* var. *lutarius* (cf. Baker and Bohling 1916; Niell et al. 1980) and others as *F. spiralis* var. *lutarius* (Kützinger) Sauvageau (cf. Sauvageau 1907; Taylor 1957). The basis of these different interpretations is their reproductive status, with unisexual plants either being designated as “typical” *F. vesiculosus* or as degenerate hermaphroditic *F. spiralis* (Sauvageau 1907). Aside from this basic reproductive interpretation of species differences, there is also support for a morphological continuum within Cotton's (1912) type material of *F. vesiculosus* var. *muscoides* from Clare Island, Ireland, as pronounced morphological variability is apparent (cf. Figure 2 in Wynne and Magne 1991). Morphological, ecological, and molecular evaluations would help to link the different muscoides-like fucoid algae to their parental plants, which could either be homogenous or heterogenous, depending upon the sites and species present.

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CHROMOSOME NUMBER DETERMINATIONS IN FAM.
COMPOSITAE, TRIBE ASTEREAEE. VI. WESTERN NORTH
AMERICAN TAXA AND COMMENTS ON GENERIC
TREATMENTS OF NORTH AMERICAN ASTERS

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ABSTRACT. Chromosome numbers are reported for 238 individuals of 79 taxa and one hybrid from 19 genera from western Canada and the western United States. The majority of the reports are for asters (109) reported in this paper under the generic names *Canadanthus*, *Eucephalus*, *Eurybia*, *Oreostemma*, *Sericocarpus*, and *Symphyotrichum* (including *Virgulus*) and gold-enrods (97) under *Solidago* and *Euthamia*. Nearly all counts confirm previous reports for the taxa; some reports are first counts for one or more of the four Canadian provinces and territories and thirteen western states of the United States sampled. The following first reports are included: *Eurybia conspicua* (*Aster conspicuus*), $2n = 126$; *Solidago simplex* var. *nana*, $2n = 18$; *Symphyotrichum falcatum* var. *falcatum*, $2n = 30$; and *S. yukonense*, $2n = 10$. The following new combinations are proposed: *Heterotheca sessiliflora* var. *echioides*, *H. sessiliflora* var. *fastigiata*, and *Oreostemma alpigenum* subsp. *haydenii*.

Key Words: Compositae, Astereae, chromosome numbers, *Aster*, *Erigeron*, *Eucephalus*, *Eurybia*, *Oreostemma*, *Sericocarpus*, *Solidago*, *Symphyotrichum*, cytotaxonomy

Determining the distribution patterns of cytotypes requires numerous counts from the range of a taxon. The determinations listed below are reported as contributions to such studies. This is the sixth in a continuing series of general reports on Astereae by the first author's laboratory (Semple 1985; Semple and Chmielewski 1987; Semple et al. 1989, 1992, 1993).

MATERIALS AND METHODS

Meiotic counts were made from pollen mother cells dissected from buds fixed in the field in 3:1 EtOH : glacial acetic acid and subsequently stored under refrigeration in 70% EtOH. Mitotic counts were made from root tip cells taken from transplanted wild rootstocks or from seedlings grown from achenes collected in the wild. Root tips were pretreated in saturated paradichlorobenzene for 2–3 hr., fixed in Acetic Alcohol Fixative (3:1 EtOH : glacial acetic acid) and hydrolyzed in 1N HCl for 30 min. at 60°C before squashing. Anther sacs containing PMCs and meristematic root tips were squashed in 1% acetic orcein, and counts of chromosomes were made from freshly prepared material. When preserved, permanent slides were made as described by Semple et al. (1981) and remain in the possession of J.C.S.

Vouchers for all counts are deposited in WAT. Identifications were made by J.C.S. Nomenclature for members of *Haplopappus sensu lato* follows Lane and Hartman (1996). In some cases, voucher specimens did not fit a published taxon description in one or more minor traits, such as amount of pubescence; these cases are indicated by the “aff.” qualifier in the Appendix.

NOMENCLATURE

The following combinations are made here.

Heterotheca sessiliflora (Nutt.) Shinnars var. ***echioides*** (Benth.) Semple, *comb. et stat. nov.* Based on *Chrysopsis echioides* Benth., Bot. Voy. Sulphur 25. 1844. *Chrysopsis villosa* (Pursh) Elliott var. *echioides* (Benth.) A. Gray, Syn. Fl. N. Amer. 1(2): 123. 1884. *Heterotheca echioides* (Benth.) Shinnars, Field & Lab. 19: 71. 1951. *Heterotheca sessiliflora* subsp. *echioides* (Benth.) Semple, Phytologia 73: 450. 1992. TYPE: U.S.A. California: Bodegas, 1841, *Hinds s.n.* (HOLOTYPE: K!).

Heterotheca sessiliflora (Nutt.) Shinnars var. ***fastigiata*** (Greene) Semple, *comb. et stat. nov.* Based on *Chrysopsis fastigiata* Greene, Pittonia 3: 296. 1898. *Chrysopsis villosa* var. *fastigiata* (Greene) H. M. Hall, Univ. Calif. Publ. Bot. 3: 43. 1907. *Heterotheca fastigiata* (Greene) V. L. Harms, Brittonia 26: 61. 1974. *Heterotheca sessiliflora* subsp. *fastigiata*

(Greene) Semple, *Phytologia* 73: 451. 1992. TYPE: U.S.A. California: San Bernardino Mts., 1000–1500 ft. (not 10,000–15,000 ft. as in protologue), 15 Oct 1895, *S. B. Parish 3815* (HOLOTYPE: NDG!; ISOTYPES: CAS!, GH!, UC!, US!)

Oreostemma alpigenum (Torr. & A. Gray) Greene subsp. ***haydenii*** (Porter) Semple, *comb. et stat. nov.* Based on *Aster haydenii* Porter, Cat. Pl. 485 in W. J. Hayden, Prelim. Rep. U.S. Geol. Surv. Montana: 485. 1872. *Oreastrum haydenii* (Porter) Rydb., Mem. New York Bot. Gard. 1: 398. 1900. *Oreostemma haydenii* (Porter) Greene, Pittonia 4: 224. 1900. *Aster alpigenus* (Torr. & A. Gray) A. Gray subsp. *haydenii* (Porter) Cronquist, Leaflet W. Bot. 5: 77. 1948. *A. alpigenus* var. *haydenii* (Porter) Cronquist, Vasc. Pl. Pacific NorthW. 5: 76. 1955. *Oreostemma alpigenum* var. *haydenii* (Porter) G. L. Nesom, *Phytologia* 74: 313. 1993. TYPE: U.S.A. Wyoming: Terr. Yellowstone R., Upper Falls, 27 Aug 1871, *F. V. Hayden 15* [LECTOTYPE, Cronquist (Leaflet W. Bot. 5: 77. 1948): US, not seen; ISOLECTOTYPES: G, GH!, PA].

RESULTS AND DISCUSSION

Chromosome numbers for 238 individuals of 79 taxa and one hybrid from 19 genera from western Canada and the western United States are reported in the Appendix. The majority of the reports are for asters and goldenrods (206); all location and voucher data are previously unpublished with the exception of one correction for a report for *Solidago nemoralis* subsp. *decemflora* (Semple et al. 1993 as *10181* in error and listed as *Semple & Zhang 10184* in the Appendix). Populations were sampled in four provinces and territories in Canada and 13 states in the United States. In total, 109 reports are for asters listed in this paper under the generic names *Canadanthus*, *Eucephalus*, *Eurybia*, *Oreostemma*, *Sericocarpus*, and *Symphyotrichum* (including *Virgulus*) and 97 goldenrods listed under *Solidago* and *Euthamia*. Nearly all counts confirm previous reports for the taxa and most are presented without comment. Included in the Appendix are the following first reports: *Eurybia conspicua*, $2n = 126$; *Solidago simplex* var. *nana*, $2n = 18$; *Symphyotrichum falcatum* var. *falcatum*, $2n = 30$; and *S. yukonense*, $2n = 10$. A number of the counts are first reports for the taxon or ploidy level of a taxon

for a particular province or state (e.g., *Oreostemma alpigenum* subsp. *alpigenum* from Oregon, $2n = 18$).

Generic limits of North American asters. In previous papers in this series, asters were placed in one of two genera: *Aster sensu lato* and *Virgulus* Raf. In this paper, a very different classification of the asters has been adopted. Xiang (1994) and Xiang and Semple (1996) presented data on chloroplast DNA restriction site variation that demonstrated conclusively that the genus *Aster sensu* Jones (1980) and *sensu* Semple and Brouillet (1980a) was polyphyletic. Nesom (1994b) presented a revised overview of the asters and made a large number of combinations in a number of the segregate genera that he recognized on morphological grounds. Other combinations had been proposed in previous papers (Nesom 1993a, 1993b, 1993c; Nesom and Leary 1992). Semple et al. (1996) proposed an alternative nomenclature in which many of the species Nesom placed in the genera *Canadanthus*, *Eurybia*, and *Symphyotrichum* (including *Virgulus*) were retained in *Aster*, while they accepted the need to recognize *Doellingeria*, *Eucephalus*, *Ionactis*, *Oreostemma*, and *Oclemena* as separate genera. The 1996 scheme is rejected here in favor of the nomenclature adopted in this paper, which by and large accepts Nesom's genera for the following reasons. In a gene sequence study testing Nesom's subtribal hypotheses (Nesom 1994a), Noyes and Rieseberg (1999) presented data that clearly demonstrated how unrelated *Symphyotrichum* is to *Aster* in the strictest sense within the tribe Astereae. They found that *Oreostemma* and *Doellingeria* are not closely related to *Aster sensu stricto*, as had Xiang and Semple (1996). As well, Xiang and Semple (1996) showed that the western North American genus *Eucephalus* is related to the eastern North American species of *Doellingeria*; Noyes and Rieseberg (1999) did not include species of *Eucephalus* in their study. Noyes and Rieseberg (1999) also showed that *Sericocarpus* is not part of *Aster sensu stricto*. Xiang and Semple (1996) found that the lectotype species *A. amellus* L. was closely related to the "eurybian" asters, which thus were thought to be best retained in the genus *Aster*. Noyes and Rieseberg (1999; nuclear DNA) did not include any "eurybian" asters in their study, but in contrast to Xiang and Semple (1996; chloroplast DNA) did find *A. amellus* to be closely related to Old World and South American genera in the tribe and not the North Amer-

ican taxa. The karyotype of *A. amellus* and those of the “eurybian” asters were found to be quite distinct (recent observations by J.C.S.); the karyotype of *A. amellus* is similar in size to that of *A. ageratoides* subsp. *ovatus* illustrated in Tara (1972), both with chromosomes larger than North American asters. Thus, after reconsideration of the morphology of the “eurybian” asters, *A. amellus*, and several other Eurasian species, and review of Nesom’s morphological observations on generic limits, we have chosen to accept inclusion of the western asters related to “*A.*” *sibiricus* in *Eurybia* as proposed by Nesom (1994b). We also have followed Nesom’s (1994b) proposal to treat *A. modestus* as *Canadanthus modestus*, although it could be included in a broadly defined *Symphyotrichum* (Semple et al. 1996; Xiang and Semple 1996). Thus, there are both morphological and molecular studies supporting the multi-generic treatment of the asters followed in this paper. Traditional treatments of *Aster* in the broad sense rest on plesiomorphies rather than true synapomorphic traits to define the genus; *Aster sensu lato* has never really been a well-defined genus. Each segregate genus as accepted here is well-defined by morphological and nucleic acid synapomorphies. A re-examination of the karyotypes of species in each genus is needed in light of the other strong evidence to determine if cytological data also are consistent with these data.

To facilitate the transition from the nomenclature accepted in previous papers in this series to what we believe will ultimately become the generally accepted nomenclature, the older names are given in brackets in the Appendix. This transition, admittedly, may be very slow in coming even though the experimental data strongly support a revised treatment. Such is the conservative nature of floristic taxonomy.

Cytotaxonomy of *Symphyotrichum yukonense*. The phylogenetic position of *Symphyotrichum yukonense* is clarified by the first chromosome number report for the species ($2n = 10$; Appendix). The mitotic karyotype of *Semple & Semple 10624* (WAT) was observed to consist of five homologues indistinguishable at the light microscope level from the published karyotype of *S. ericoides* (Semple 1976; reported as *Aster ericoides*). This is the “virguloid” karyotype shared by all $x = 5$ members of *Symphyotrichum* subg. *Virgulus* (Semple and Brouillet 1980b, under the generic name *Lasallea*; Semple et al. 1983). This is a straight-

forward case of classical cytotaxonomic methods being sufficient to resolve a phylogenetic question because the karyotype is so obviously “virguloid.” Had the chromosome number been $2n = 18$, then other methods would likely have been required to reveal the phylogenetic relationships of the species. In the protologue of the species, Cronquist (1945) considered *S. yukonense* to be related to *S. novae-angliae* ($2n = 10$) and *Canadanthus modestus* ($2n = 18$) based on similar involucre traits and only superficially similar to *S. campestre* (all species discussed under the generic name *Aster*). Hultén (1968) suggested that *S. yukonense* was close to *Aster pygmaeus* Lindl. in Hook. [synonyms: *A. sibiricus* L. subsp. *pygmaeus* (Lindl. in Hook.) Löve & Löve; *Eurybia pygmaea* (Lindl. in Hook.) G. L. Nesom]. Jones (1980) included *S. yukonense* in subg. *Virgulus* with a “?” and the comment “perhaps = *campestris*”. Semple and Brouillet (1980a) did not comment on the species and did not include it in their emended treatment of *Lasallea* Greene, which was subsequently replaced by the older name *Virgulus* Raf. (Reveal and Keener 1981). Nesom (1994a) transferred the species from *Aster* to *Symphyotrichum* without comment, although its inclusion in the latter genus in subsect. *Polyligulae* (Semple) G. L. Nesom is obviously implicitly based on Nesom’s recognition of its morphological similarities to the other species he included: *S. novae-angliae* (type), *S. campestre*, *S. fendleri*, and *S. oblongifolium*. The karyotypes ($2n = 10$) of *S. novae-angliae*, *S. campestre*, *S. fendleri*, and *S. oblongifolium* are essentially identical to that of *S. yukonense*. *Canadanthus modestus* ($2n = 18$) is the type species of Nesom’s monotypic genus *Canadanthus*; its karyotype is distinct from the $x = 8$ karyotypes of *Symphyotrichum* subg. *Symphyotrichum* and the $x = 5$ karyotypes of the virguloid asters of *S.* subg. *Virgulus* (Semple 1984; Semple and Brouillet 1980b; Semple et al. 1983). Based on the karyotype and observations on morphology of *S. yukonense* in the field, it seems likely that the species is derived from *S. campestre*, which has been observed growing near lakes in western North America. Small population sizes and a marginal habitat for a virguloid aster resulted in the evolution of a distinct diminutive species endemic to a few locations in the Yukon and Alaska. Long distance dispersal by birds may account for its original arrival in the far north and subsequent disjunct distribution.

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APPENDIX

CHROMOSOME NUMBER DETERMINATIONS OF ASTEREAEE

Chromosome number determinations of Astereae from Canada and the United States are arranged alphabetically by species. *Ah* = T. Ahmed; *Ch* = J. Chmielewski; *Hd* = S. Heard; *S* = J. Semple; *S & S* = J. and B. Semple; *Su* = Bambang Agus Suripto; *Xg* = ChunSheng Xiang; *Zh* = Jie Zhang. When voucher specimens did not fit a published taxon description in one or more minor traits, the “aff.” qualifier is used.

- Canadanthus modestus* (Lindl.) G. L. Nesom [*Aster modestus* Lindl.]. — $2n = 18$. CANADA. Alberta: City of Fox Creek, Hwy. 3, *Emery & Emery 15*. British Columbia: Cassier Hwy. (KP275), along Beaverpond Creek, just N of Ningunsaw Summit, *S & S 10633*; Yellowhead Hwy. (Hwy.-16) E of Hazelton (KP302), 2 km W of China Creek, *S & S 10636*; Hwy.-16, vicinity of rest area, ca. 11 km E of Burns Lake, *S & S 10638*; Hwy.-16 10 km S of Macbride, by Holmes River, *S & S 10639*. U.S.A. Idaho: Idaho Co., SW of Lolo Pass, DeVoto Mem. Cedar Grove, *S & Xg 10309*. Montana: Broadwater Co., E of Townsend, Belt Mts., For. Rd.-423, *S & Xg 10328*; Gallatin Co., N of Bozeman and W of Wilsall, Gallatin Nat'l. For., For. Rd.-642 by Sixteen Mile Creek, *S & Xg 10244*; Missoula Co., NE of Lolo Pass, Lee Creek, S of Lolo Hot Springs, *S & Xg 10311*. Oregon: Clackamas Co., Mt. Hood Nat'l. For., For. Hwy.-42, Clackamas Meadow, *S & Xg 10269*. Washington: Chelan Co., US-12 below Stevens Pass, above For. Rd.-6970, *S & Xg 10296*; Clallam Co., Olympic Peninsula, E of Forks, junct. For. Hwy.-29 and For. Rd.-2932 (T29N R12W S6), *S & Xg 10281*; Whatcom Co., Mt. Baker, N side, WA-542, *S & Xg 10290*; Yakima Co., WA-410 4.1 km W of Mt. Ranier Nat'l Park, *S & Xg 10307*.
- Chrysothamnus viscidiflorus* (Hook.) Nutt. var. *lanceolatus* (Nutt.) Greene. — $2n = 9_{II}$. U.S.A. Utah: Summit Co., just E of UT-150 on For. Rd., 10.0 km S of state line, *S, Su & Ah 9212*.
- C. viscidiflorus* (Hook.) Nutt. var. *puberulus* (D. C. Eaton) Jepson. — $2n = 18_{II}$. U.S.A. Utah: Salt Lake–Wasatch Co. line, UT-90, pass E of Brighton, *S, Su & Ah 9250*.
- Corethrogyne filaginifolia* (Hook. & Arn.) Nutt. — $2n = 5_{II}$. U.S.A. California: San Benito Co., New Idria Mine Camp 2 Pit, *S, Su & Ah 9357*.
- Ericameria bloomeri* (A. Gray) J. F. Macbr. var. *bloomeri*. — $2n = 18_{II}$. U.S.A. California: Sierra Co., Nichols Mill Rd. (For. Rd.-15) 2.3 km E of Yuba Pass Rd. (For. Rd.-12), *S, Su & Ah 9328*.
- Erigeron arenarioides* (D. C. Eaton) A. Gray. — $2n = 9_{II}$. U.S.A. Utah: Salt Lake Co., UT-190 E of Midvale, Big Cottonwood Canyon, Wasatch Nat'l For., Mill B. Picnic Area, *S, Su & Ah 9242*.
- E. caespitosus* Nutt. — $2n = 9_{II}$. U.S.A. Wyoming: Albany Co., E of Laramie, ridge by Happy Jack Rd., S of Lincoln Monument on I-80, *S & S 10360*. — $2n = 18$. Montana: Carbon Co., SW of Red Lodge, For. Rd.-421 at Wyoming Creek, in Limber Pine Nat'l. For. Campground (T9S R19E S8), *S & Xg 10237*.
- E. compositus* Pursh. — $2n = 18$. U.S.A. Wyoming: Albany Co., Snowy Mts., WY-130, Libby Flats Observation Tower, *S & Zh 10408*. — $2n = 36$. Colorado: Pitkin Co., Independence Pass, *S & Zh 10458*.
- E. glaucus* Ker Gawl. — $2n = 9_{II}$. U.S.A. California: Marin Co., Tomales Pt., lower cliffs at McClures Beach, *S, Su & Ah 9330*.
- E. peregrinus* (Pursh) Greene var. *callianthemus* Cronquist. — $2n = 36$. U.S.A. Wyoming: Park Co., US-12, 2 km E of Long Lake, Bear-tooth Range, *S & Zh 10426*.
- E. peregrinus* (Pursh) Greene var. *dawsonii* Greene. — $2n = 36$. U.S.A.

- Washington: Whatcom Co., Mt. Baker, Ptarmigan Ridge Trail, *S* & *Xg* 10293.
- E. peregrinus* (Pursh) Greene var. *scaposus* (Torr. & A. Gray) Cronquist. — $2n = 18$. U.S.A. Oregon: Hood River Co., Mt. Hood, along creek below tree line, below Eliot Glacier, *S* & *Xg* 10275. Washington: Whatcom Co., Mt. Baker, Ptarmigan Ridge Trail, *S* & *Xg* 10295.
- E. speciosus* (Lindl.) DC. — $2n = 18$. U.S.A. New Mexico: Lincoln Co., W of Alto, NM-532 at Oak Grove Campground, *S* & *Hd* 8119. Wyoming: Johnson Co., Powder River Pass, Middle Fork Clear Creek Campground, *S* & *Xg* 10207.
- E. subtrinervis* Rydb. — $2n = 18$. U.S.A. Wyoming: Carbon Co., NW of Battle Mt., For. Rd.-801 by For. Rd.-801.18, ca. 10 km N of WY-70, *S* & *Zh* 10415.
- E. ursinus* D. C. Eaton. — $2n = 9_{II}$. U.S.A. Colorado: Pitkin Co., Independence Pass, *S* & *Zh* 10456.
- Eucephalus breweri* (A. Gray) G. L. Nesom [*Aster breweri* (A. Gray) Semple]. — $2n = 9_{II}$. U.S.A. California: Nevada Co., I-80, Donner Summit Rest Area, W of Donner Lake, *S* & *S* 10359.
- E. engelmannii* (D. C. Eaton) Greene [*Aster engelmannii* (D. C. Eaton) A. Gray]. — $2n = 9_{II}$. U.S.A. Washington: Chelan Co., W of Merrit, Merrit Lake Trail Rd., just S of US-12, *S* & *Xg* 10297.
- E. glaucescens* (A. Gray) Greene [*Aster glaucescens* (A. Gray) S. F. Blake]. — $2n = 9_{II}$. U.S.A. Washington: Klickitat Co., NW of Humsum, W of Mt. Baldy, ca. 3 km W of WA-141 on gravel side rd., *S* & *Xg* 10273.
- E. glaucus* Nutt. [*Aster glaucodes* S. F. Blake]. — $2n = 9_{II}$. U.S.A. Colorado: Garfield Co., 6 km S of county line, CO-139 just N of Douglas Pass, *S* & *Zh* 10444; Pitkin Co., CO-82 6.6 km E of Aspen, *S* & *Zh* 10448. Utah: Salt Lake Co., E of Midvale, UT-190, Big Cottonwood Canyon, *S*, *Su* & *Ah* 9244. Wyoming: Teton Co., E of Hoback Junction, US 191 2 km E of Hoback campground, *S* & *Zh* 10439.
- E. ledophyllus* (A. Gray) Greene var. *covillei* (Greene) G. L. Nesom [*Aster ledophyllus* A. Gray var. *covillei* (Greene) Cronquist]. — $2n = 9_{II}$. U.S.A. Oregon: Jefferson Co., US-20 just E of Santiam Pass, woods, 4800 ft. el., *S* & *Xg* 10262.
- Eurybia conspicua* (Lindl.) G. L. Nesom [*Aster conspicuus* Lindl.]. — $2n = \text{ca. } 108$. CANADA. Alberta: Hwy.-43 16.4 km W of Little Smoky, *S* & *S* 10608. U.S.A. Montana: Broadwater Co., E of Townsend, Belt Mts., For. Rd.-423, *S* & *Xg* 10323, *S* & *Xg* 10330. Washington: Chelan Co., US-97 22.2 km S of US-2, *S* & *Xg* 10303. — $2n = 126$. CANADA. Alberta: Hwy.-16, vicinity of rest area ca. 11 km E of Burns Lake, *S* & *S* 10637.
- E. merita* (A. Nelson) G. L. Nesom [*Aster meritus* A. Nelson]. — $2n = 36$. U.S.A. Montana: Carbon Co., US-212 N of Beartooth Pass, vicinity of hairpin turn, *S* & *Xg* 10232; below summit near tree line, *S* & *Zh* 10421; 2.8 km W of Cooke City, *S* & *Zh* 10431; SW of Red Lodge, For. Rd.-421 at Wyoming Creek, in Limber Pine Nat'l. For. Campground (T9S R19E S8), *S* & *Xg* 10234. Wyoming:

Johnson Co., US-16 just W of Powder River Pass, *S* & *Xg* 10219; Washakie Co., Big Horn Mts., US-16 1.8 km S of county line (T48N R86W S6), *S* & *Xg* 10221.

E. radulina (A. Gray) G. L. Nesom [*A. radulinus* A. Gray]. — $2n = 9_{II}$. U.S.A. California: Contra Costa Co., Charles Tilden Reg. Park, Vollmer Peak, *S*, *Su* & *Ah* 9340.

E. sibirica (L.) G. L. Nesom [*Aster sibiricus* L.]. — $2n = 18$. CANADA. British Columbia: Buckinghorse, Buckinghorse Prov. Park, along river, *S* & *S* 10615. Yukon Territory: Hwy.-2 ca. 20 km E of Dawson City, banks of Klondike River, *S* & *S* 10628; Klondike Loop Hwy., W of Stewart Crossing (KP543), *S* & *S* 10627; between Whitehorse and Haines Junction, Alaska Hwy. (KP1557), banks of Mendenhall River, *S* & *S* 10625.

Euthamia occidentalis Nutt. — $2n = 18$. U.S.A. California: Plumas Co., Taylorville, County Park, gravel bars of Indian Creek, *S*, *Su* & *Ah* 9308; San Benito Co., W of Hernandez, Coalinga Rd. by Laguna Creek, *S*, *Su* & *Ah* 9348. Nevada: Humboldt Co., NV-140, 31 mi. SE of Denio, N of Jackson Mt., vicinity of irrigation ditch, *S*, *Su* & *Ah* 9288.

Grindelia squarrosa (Pursh) Dunal. — $2n = 6_{II}$. U.S.A. Utah: Salt Lake Co., UT-190 E of Midvale, lower end of Big Cottonwood Canyon, *S*, *Su* & *Ah* 9240.

Gutierrezia sarothrae (Pursh) Britton & Rusby. — $2n = 4_{II}$. U.S.A. Wyoming: Carbon Co., WY-130 at Co. Rd.-209, 2.3 km E of WY-230, *S* & *Zh* 10410.

Heterotheca fulcrata (Greene) Shinnery var. *senilis* (Wooton & Standl.) Semple. — $2n = 9_{II}$. U.S.A. New Mexico: Doña Ana Co., E slope of Organ Mts., SE of Organ, *S* & *S* 10510.

H. oregona (Nutt.) Shinnery var. *scaberrima* (A. Gray) Semple. — $2n = 9_{II}$. U.S.A. California: Monterey Co., W of Greenfield, gravel bars of Arroyo Seco River by Hwy. G-16 bridge, *S* & *S* 10478.

H. sessiliflora (Nutt.) Shinnery var. *echioides* (Benth.) Semple. — $2n = 9_{II}$. U.S.A. California: Ventura Co., SE of Venticopa, *S et al.* 5634.

H. sessiliflora (Nutt.) Shinnery var. *fastigiata* Semple. — $2n = 9_{II}$. U.S.A. California: Los Angeles Co., N of Claremont, Mt. Baldy Rd. just S of L.A. Nat'l. For. boundary, *S* & *Ch* 8629.

H. villosa (Pursh) Shinnery var. *scabra* (Eastw.) Semple. — $2n = 9_{II}$. U.S.A. Utah: Salt Lake Co., UT-190 E of Midvale, Big Cottonwood Canyon, Mill B. Picnic Area, *S*, *Su* & *Ah* 9247.

Isocoma menziesii (Hook. & Arn.) G. L. Nesom var. *menziesii*. — $2n = 6_{II}$. U.S.A. California: San Benito Co., New Idria Rd., Griswald Canyon, S of Panoche, *S*, *Su* & *Ah* 9358.

Machaeranthera canescens (Pursh) A. Gray var. *latifolia* (A. Nelson) S. L. Welsh. — $2n = 4_{II} + 1_{II}$ supernumeraries. U.S.A. Utah: Salt Lake Co., UT-190 at pass E of Brighton, Wasatch Co. line, *S*, *Su* & *Ah* 9249.

M. gracilis (Nutt.) Shinnery. — $2n = 2_{II}$. U.S.A. New Mexico: Grant Co., frontage rd. just W of Separ Exit on I-10, *S* & *S* 10507.

Oreostemma alpigenum (Torr. & A. Gray) Greene subsp. *alpigenum*

- [*Aster alpigenus* (Torr. & A. Gray) A. Gray subsp. *alpigenus*]. —
 $2n = 18$. U.S.A. Oregon: Hood River Co., Mt. Hood, Cooper Spur
 Trail below Eliot Glacier, *S* & *Xg* 10271.
- O. alpigenum* (Torr. & A. Gray) Greene subsp. *haydenii* (Porter) Semple
 [*Aster alpigenus* (Torr. & A. Gray) A. Gray subsp. *haydenii* (Porter)
 Cronquist]. — $2n = 18$. U.S.A. Wyoming: Park Co., Bear Tooth
 Mts., Gardner Lake Trail trailhead, *S* & *Zh* 10419; US-212 2 km
 E of Long Lake, *S* & *Zh* 10424.
- Pyrrocoma apargioides* (A. Gray) Greene. — $2n = 6_{II}$. U.S.A. Califor-
 nia: Plumas Co., Sierra Valley, A-24 just W of CA-49, 8 km N of
 Loyalton, *S*, *Su* & *Ah* 9315.
- P. lanceolata* (Hook.) Greene. — $2n = 12_{II}$. U.S.A. Nevada: Elko Co.,
 17 mi. NE of Ruby Valley, by NV-229 in dry bed of Franklin River,
 E of Ruby Dome, *S*, *Su* & *Ah* 9366.
- P. racemosa* (Nutt.) Torr. & A. Gray var. *racemosa*. — $2n = 6_{II}$. U.S.A.
 California: San Benito Co., Clear Creek Rd. 4.65 km E of Coalinga
 Rd., *S*, *Su* & *Ah* 9350.
- Sericocarpus oregonensis* Nutt. subsp. *californicus* (Durand) Ferris [*As-
 ter oregonensis* (Nutt.) Cronquist subsp. *californicus* (Durand)
 Keck]. — $2n = 9_{II}$. U.S.A. California: Placer Co., I-80, Rest Area
 E of Gold Run, *S* & *S* 10358.
- S. oregonensis* Nutt. subsp. *oregonensis*. [*Aster oregonensis* (Nutt.)
 Cronquist subsp. *oregonensis*]. — $2n = 9_{II}$. U.S.A. Oregon: Marion
 Co., W of Detroit, Hall Ridge Rd., Willamette Nat'l. For. (T10S
 R5E S17), *S* & *Xg* 10267.
- Solidago altissima* L. var. *gilvocanescens* (Rydb.) Semple. — $2n = 18$.
 CANADA. Manitoba: S of Winnipeg, MB-75 1 km N of Hwy.-
 305, NW of Ste. Agathe, *S* 10645. — $2n = 36$. U.S.A. Wyoming:
 Carbon Co., S of Arlington, ca. 2.3 km S of I-80, Rocky Creek
 Trail, *S*, *Su* & *Ah* 9208, *S*, *Su* & *Ah* 9210; Crook Co., W of Moor-
 croft, I-90-bus. right-of-way, *S* & *Xg* 10193.
- S. californica* Nutt. — $2n = 18$. U.S.A. California: Kern Co., CA-155
 1.6 km E of Glennville, *S* & *Ch* 8947; CA-178 between Onyx and
 Weldon, *S*, *Su* & *Ah* 9365; Plumas Co., CA-89 10.5 km NW of
 Greenville, *S*, *Su* & *Ah* 9303; Taylorville, County Park, edge of
 Indian Creek, *S*, *Su* & *Ah* 9307; San Benito Co., W of Sweetwater
 Spring, Coalinga Rd., Lorenzo Vasques Canyon, ca. S of Black Mt.
 radio tower, *S*, *Su* & *Ah* 9346; Shasta Co., W of Fall River Mills,
 CA-299, 2.5 km E of Pit River, *S*, *Su* & *Ah* 9300.
- S. canadensis* L. subsp. *elongata* (Nutt.) Keck. — $2n = 18$. U.S.A. Cal-
 ifornia: Modoc Co., NE of Alturas, US-395 ca. 2 km S of Joseph
 Creek Rd., along N. Fork Pit River, *S*, *Su* & *Ah* 9295, *S*, *Su* & *Ah*
 9296, *S*, *Su* & *Ah* 9297. Washington: Clallam Co., Olympic Pen.,
 E of Forks, For. Rd.-2932 (T29N R12W S17, NE corner), *S* & *Xg*
 10279; Grays Harbor Co., N of Huguam, US-101 (MP100) 14.6
 km S of Humptulips River, *S* & *Xg* 10278; Whatcom Co., N of
 Mt. Baker, WA 542 S of Silver Fir Campground, *S* & *Xg* 10289.
 — $2n = 36$. CANADA. British Columbia: E of Hazelton, Yellow-
 head Hwy.(16), KP302, 2 km W of China Creek, *S* & *S* 10635.

- S. canadensis* L. subsp. *salebrosa* (Piper) Keck. — $2n = 18$. U.S.A. Colorado: Gunnison Co., 3.3 km W of Crested Butte, Kebler Pass Rd., *S* & *Hd* 7754. Idaho: Owyhee Co., W of Silver City, Silver City Rd. E of strip mine, along Jordan Creek, *S* & *Xg* 10258. Wyoming: Carbon Co., S of Arlington, ca. 2.3 km S of I-80, Rocky Creek Trail, *S*, *Su* & *Ah* 9209. — $2n = 36$. U.S.A. Montana: Carbon Co., MT-78 1.6 km NW of Red Lodge, *S* & *Xg* 10239. — $2n = 54$. CANADA. Alberta: AB-43 E of Grand Prairie, W of Bezanson, *S* & *S* 10612. U.S.A. Montana: Broadwater Co., E of Townsend, Belt Mts., For. Rd.-423 at Edith Lake Rd., *S* & *Xg* 10324. Utah: Salt Lake Co., E of Midvale, UT-190, Big Cottonwood Canyon, *S*, *Su* & *Ah* 9245; Summit Co., UT-150 (MP 5.5) W of Kamas, *S*, *Su* & *Ah* 9238. Washington: Chelan Co., NW of Leavenworth, US-2 0.8 km SE of WA-207 (Coles Corner), *S* & *Xg* 10298, *S* & *Xg* 10299. Wyoming: Uintah Co., WY-150 ca. 11.5 km S of Evanston, by creek S of Bear River, *S*, *Su* & *Ah* 9211.
- S. confinis* Nutt. — $2n = 18$. U.S.A. California: San Benito Co., W of Hernandez, Coalinga Rd. at Laguna Creek, *S*, *Su* & *Ah* 9347.
- S. gigantea* Aiton (“*shinneryi*” morph). — $2n = 54$. U.S.A. Montana: Broadwater Co., Belt Mts., E of Townsend, banks of East Fork of Deep Creek, For. Rd.-423, *S* & *Xg* 10329; Gallatin Co., N of Bozeman and W of Wilsall, Gallatin Nat'l. For., For. Rd.-642, along Sixteenmile Creek, *S* & *Xg* 10243; Powell Co., MT-20 17.7 km W of Lincoln, *S* & *Xg* 10312.
- S. aff. gigantea* Aiton. — $2n = 54$. U.S.A. California: Modoc Co., NE of Alturas, US-395 ca. 2 km S of Joseph Creek Rd., along North Fork of Pit River, *S*, *Su* & *Ah* 9294.
- S. guiradonis* A. Gray. — $2n = 18$. U.S.A. California: San Benito Co., Clear Creek Rd. 4.6 km N of Coalinga Rd., *S*, *Su* & *Ah* 9351-A; 3.5 km S of New Idria, junct. of Clear Creek Rd. and Saw Mill Creek Rd., San Carlos Creek, *S*, *Su* & *Ah* 9356-C.
- S. lepida* DC. — $2n = 36$. CANADA. Yukon Territory: Alaska Hwy. (KP1400.3), NW of Jakey, 23 km S of Judas Creek, *S* & *S* 10622. — $2n = 54$. CANADA. British Columbia: Alaska Hwy. (BC-97) 13.0 km W of Toad River, *S* & *S* 10618; Little Smoky, just S of town, *S* & *S* 10607.
- S. missouriensis* Nutt. — $2n = 18$. U.S.A. Idaho: Owyhee Co., Owyhee Mts., Silver City Range, Silver City Rd. 22 km SE of ID-78, *S* & *Xg* 10257. Nevada: Humboldt Co., NV-140 31 mi. SE of Denio, N of Jackson Mt., vic. of irrigation ditch, *S*, *Su* & *Ah* 9290. Wyoming: Crook Co., E of Sundance, US-14 right-of-way by I-90 exit, *S* & *Xg* 10187; Park Co., US 212 7 km W of WY-296, *S* & *Zh* 10430. — $2n = 36$. Montana: Broadwater Co., E of Townsend, W slopes of Belt Mts., For. Rd.-423, *S* & *Xg* 10316; Carbon Co., SW of Red Lodge, For. Rd.-421 at Wyoming Creek, in Limber Pine Nat'l. For. Campground, *S* & *Xg* 10233. Nevada: Elko Co., Ruby Mts., E of NV-227, Soldier Creek Trail, lower el., near end of jeep trail, *S*, *Su* & *Ah* 9272; mid el., *S*, *Su* & *Ah* 9277; upper mid el., *S*, *Su* & *Ah* 9279, *S*, *Su* & *Ah* 9280. Wyoming: Carbon Co., S of

- Arlington, vicinity of gravel rd. by I-80 exit, *S*, *Su* & *Ah* 9204; Johnson Co., N of Buffalo, E of Lake Smet, Bellus Rd. (T52N R82W S13), *S* & *Xg* 10195; W of Buffalo, US-16 (MP83) 5.5 km E of Hunter Rd., *S* & *Xg* 10205.
- S. mollis* Bartl. var. *mollis*. — $2n = 18_{II}$. U.S.A. Wyoming: Crook Co., E of Sundance, US-14, vicinity of entrance to I-90, *S* & *Xg* 10188. — $2n = 36$. South Dakota: Minnehaha Co., NW of Humbolt, SD-38 3.5 km W of SD-19, *S* & *Xg* 10181.
- S. multiradiata* Aiton. — $2n = 18$. CANADA. British Columbia: Cassier Hwy. ca. 25 km S of Dease Lake, KP460, S of Gnat Summit, *S* & *S* 10632. U.S.A. Colorado: Pitkin Co., Independence Pass, *S* & *Zh* 10460. Utah: Summit Co., W of Kamas, UT-150 along Slate Creek, *S*, *Su* & *Ah* 9228; UT-150, East Fork Bear River Campground, *S*, *Su* & *Ah* 9215; Duchesne Co. line, peak W of Highline Trailhead on UT-150, *S*, *Su* & *Ah* 9227. Washington: Clallam Co., S of Port Angeles, Olympic Mts., between Eagle Pt. and Obstruction Peak, *S* & *Xg* 10287. Wyoming: Albany Co., Snowy Mts., WY-130 18 km W of Centennial, rd. to Sugarloaf Rec. Area, *S* & *Zh* 10406; Carbon Co., Battle Mt., WY-70, Battle Pass, *S* & *Zh* 10414. — $2n = 36$. Montana: Carbon Co., N of Beartooth Pass, US-212 near hairpin turn, 8155 ft. el., *S* & *Xg* 10231. Wyoming: Park Co., Beartooth Range, US-212 E of Beartooth Pass, Beartooth Loop above Gardner Lake (T58N R104W S29), *S* & *Xg* 10227; US-212 E of Long Lake, *S* & *Zh* 10423.
- S. nana* Nutt. — $2n = 18$. U.S.A. Utah: Summit Co., W of Kamas, UT-150 along Slate Creek, *S*, *Su* & *Ah* 9235.
- S. nemoralis* Aiton subsp. *decemflora* (DC.) Brammall ex Semple. — $2n = 18_{II}$. U.S.A. Colorado: Sedgwick Co., S of Julesburg, US-385 just S of I-76, *S* & *Zh* 10472. South Dakota: Minnehaha Co., NW of Humboldt, SD-38 3.5 km W of SD-19, *S* & *Zh* 10184 [published in Semple et al. 1993 in error as 10181, see *S. mollis* above]
- S. parryi* (A. Gray) Greene. — $2n = 18$. U.S.A. New Mexico: McKinley Co.—Valencia Co. line, N of Grants, San Mateo Spring Canyon, SW of Springs (T12N R7W S7), *S*, *Su* & *Ah* 9371; Valencia Co., Cebolleta Mts., Mt. Taylor ca. 10,700 ft. el. (T12N R7W S20), *S*, *Su* & *Ah* 9378. Utah: Salt Lake Co., Brighton, *S*, *Su* & *Ah* 9248; Summit Co., UT-150 (MP38) ca. 30 km S of Wyoming state line, *S*, *Su* & *Ah* 9222. Wyoming: Carbon Co., Battle Mt., WY-70, Battle Pass, *S* & *Zh* 10413.
- S. rigida* L. subsp. *humilis* (Porter) S. B. Heard & Semple. — $2n = 18$. U.S.A. Montana: Carbon Co., MT-78 1.6 km NW of Red Lodge, *S* & *Xg* 10238. Wyoming: Johnson Co., N of Buffalo, E of Lake Smet, Bellus Rd. (T52N R82W S13), *S* & *Xg* 10196.
- S. simplex* Kunth (subsp. *simplex*) var. *nana* (A. Gray) Ringius. — $2n = 18$. U.S.A. Oregon: Hood River Co., Mt. Hood, Cooper Spur Trail below Eliot Glacier, *S* & *Xg* 10270.
- S. simplex* Kunth (subsp. *simplex*) var. *simplex*. — $2n = 18$. CANADA. British Columbia: Cassier Hwy. (Hwy.-37) 80 km S of Alaska Hwy., KP643.5, ca. 5 km N of Boya Lake, *S* & *S* 10631. Yukon

Territory: Alaska Hwy. just N of Haines Junction, *S* & *S* 10623; Klondike Loop (YT-2), KP270, N of Fox Lake, *S* & *S* 10626. U.S.A. Colorado: Pitkin Co., CO-82 16 km E of Aspen, just E of For. Rd.-106, *S* & *Zh* 10450. New Mexico: McKinley Co.—Valencia Co. line, SE of San Mateo, San Mateo Rd., Cibola Nat'l. For. (T12N R7W S5), *S*, *Su* & *Ah* 9368; N of Grants, San Mateo Spring Canyon, SW of Springs (T12N R7W S7), *S*, *Su* & *Ah* 9370, *S*, *Su* & *Ah* 9372; Valencia Co., Cebolleta Mts., Mt. Taylor ca. 10,700 ft. el. (T12N R7W S120), *S*, *Su* & *Ah* 9379; 10,500 ft. el., *S*, *Su* & *Ah* 9380. Wyoming: Johnson Co., W of Buffalo, US-16 between Pole Creek and Caribou Creek, N of Crazy Woman Campground, *S* & *Xg* 10211.

S. sparsiflora A. Gray. — $2n = 18$. U.S.A. New Mexico: Bernalillo Co., NM-14 S of Tijeras, *S*, *Su* & *Ah* 9382; Lincoln Co., W of Alto, NM-532 at Oak Grove Campground, *S* & *Hd* 8121. Wyoming: Fremont Co., WY-287 E of Jeffrey City, Split Rock Historical Marker Site, *S* & *Zh* 10418. — $2n = 36$. Colorado: Garfield Co., CO-139 just N of Douglas Pass, 6 km S of county line, *S* & *Zh* 10445. Utah: Salt Lake Co., E of Midvale, UT-190 3.5 mi E of UT-210, lower end of Big Cottonwood Canyon, *S*, *Su* & *Ah* 9241. Wyoming: Teton Co., Gros Ventre Rd. 8 km E of Kelly, Lower Slide Lake Campground, *S* & *Zh* 10437.

S. spectabilis (D. C. Eaton) A. Gray. — $2n = 18$. U.S.A. California: Sierra Co., S of Loyalton, Antelope Valley Rd. SW of Sierra Brooks, *S*, *Su* & *Ah* 9316.

S. wrightii A. Gray. — $2n = 9_{II}$. U.S.A. Arizona: Gila Co., near Salt River below US-60 bridge, *S* & *S* 10496. — $2n = 18$. Texas: Culberson Co., Guadalupe Mt. Nat'l. Park, Bowl Trail, 7880 ft. el., *S* & *Hd* 8185 (collected under permit from GMNP).

Symphyotrichum ascendens (Lindl.) Nees [syn: *Aster ascendens* Lindl.]. — $2n = 26$. U.S.A. California: Sierra Co., CA-49 W of Yuba Pass, *S* & *Hd* 8407; Yuba Pass Rd. ca. 2.5 km N of Nichol Mill Rd., *S*, *Su* & *Ah* 9323. — $2n = 52$. Colorado: Gunnison Co., US-50 just W of Gunnison city limits, by museum, *S* & *Hd* 7750; E of Somerset, Kebler Pass Rd. 3.0 km E of CO-133, *S* & *Hd* 7785; 20 km E of CO-133, *S* & *Hd* 7777. Montana: Broadwater Co., E of Townsend, W slopes of Belt Mts., For. Rd.-423, *S* & *Xg* 10321. Wyoming: Johnson Co., W of Buffalo, US-16 (MP83) 5.5 km E of Hunter Rd., *S* & *Xg* 10204. — $2n = 52 + 2$ supernumeraries. Montana: Broadwater Co., E of Townsend, W slopes of Belt Mts., For. Rd.-423, *S* & *Xg* 10319.

S. campestre (Nutt.) G. L. Nesom [*Aster campestris* Nutt.]. — $2n = 5_{II}$. U.S.A. Montana: Beaverhead Co., WSW of Grant, MT-324 S of Lemhi Pass Rd., *S* & *Xg* 10249. — $2n = 10$. Montana: Lewis and Clark Co., E of Lincoln, MT-279, Flesher Pass, *S* & *Xg* 10315.

S. chilense (Nutt.) G. L. Nesom [*Aster chilensis* Nees]. — $2n = 48$. U.S.A. California: Contra Costa Co., E of Berkeley, Berkeley Hills, Grizzly Peak Rd., *S*, *Su* & *Ah* 9337; Del Norte Co., E of Klamath,

- bluff along N side of Klamath River, *S* & *Hd* 8516; Mendocino Co., CA-1, 10 km N of Cleone, *S* & *Hd* 8538.
- S. ciliolatum* (Lindl.) Löve & Löve [*Aster ciliolatus* Lindl.]. — $2n = 48$. CANADA. Alberta: Little Smoky, just S of town on side rd., *S* & *S* 10605. British Columbia: Alaska Hwy. (BC-97), KP46, near brake test area, *S* & *S* 10614; 10.8 km W of Smith River bridge, *S* & *S* 10619; 13.0 km W of Toad River, *S* & *S* 10617; Buckinghorse, Buckinghorse Prov. Park, *S* & *S* 10616; Cassier Hwy. (BC-37), KP87, 10.6 km N of Cranberry River bridge, *S* & *S* 10634; Yellowhead Hwy., McBride, *Emery* & *Emery* 3a. U.S.A. Wyoming: Washakie Co., Bighorn Mts., Tensleep Canyon, Leigh Campground, *S* & *Xg* 10222.
- S. eatonii* (A. Gray) G. L. Nesom [*Aster bracteolatus* Nutt.; *A. eatonii* A. Gray]. — $2n = 16$. U.S.A. California: Modoc Co., NE of Alturas, flood plain of North Fork of Pit River along US-395, ca. 2 km S of Joseph Creek Rd., *S*, *Su* & *Ah* 9298. Montana: Broadwater Co., E of Townsend, Belt Mts., For. Rd.-423 along East Fork of Deep Creek, *S* & *Xg* 10326. Washington: Chelan Co., NW of Leavenworth, US-2 0.8 km SE of Coles Corner (WA-207), *S* & *Xg* 10300; Kittitas Co., US-97 10.8 km by rd. W of Swauk Pass, N of Durst Creek Rd. (For. Rd.-9705), *S* & *Xg* 10304.
- S. ericoides* (L.) G. L. Nesom var. *ericoides* [*Aster ericoides* L. var. *ericoides*]. — $2n = 10$. CANADA. Alberta: AB-43 E of Grand Prairie, W of Bezanson, *S* & *S* 10609. — $2n = 20$. U.S.A. South Dakota: Minnehaha Co., NW of Humboldt, SD-38 3.5 km W of SD-19, *S* & *Xg* 10180.
- S. falcatum* (Lindl.) G. L. Nesom var. *commutatum* (Torr. & A. Gray) Nesom [*Aster falcatus* Lindl. var. *commutatum* Torr. & A. Gray]. — $2n = 30$. CANADA. Alberta: N of Drumheller, Midland Prov. Park, near Red Deer River, *S* 10641. U.S.A. Montana: Broadwater Co., E of Townsend, W slopes of Belt Mts., For. Rd.-423, *S* & *Xg* 10318; Gallatin Co., N of Bozeman and W of Wilsall, For. Rd. 6.2 km W of MT-86, *S* & *Xg* 10242. Wyoming: Carbon Co., WY-130 at Co. Rd.-209, 2.3 km W of WY-230, *S* & *Zh* 10411; Johnson Co., N of Buffalo, E of Lake Smet, Bellus Rd., *S* & *Xg* 10197; S of Lake Smet, *S* & *Xg* 10200; W of Buffalo, US-16 5.5 km E of Hunter Rd., *S* & *Xg* 10203; Washakie Co., Big Horn Mts., Tensleep Canyon, Leigh Campground, *S* & *Xg* 10223.
- S. falcatum* (Lindl.) G. L. Nesom var. *falcatum* [*Aster falcatus* Lindl. var. *falcatus*]. — $2n = 30$. CANADA. Alberta: N of Drumheller, Midland Prov. Park, rd. embankment, *S* 10643.
- S. foliaceum* (Lindl.) G. L. Nesom [*Aster foliaceus* Lindl.]. — $2n = 16$. U.S.A. Montana: Broadwater Co., E of Townsend, Belt Mts., For. Rd.-423, bank of East Fork of Deep Creek, *S* & *Xg* 10327; Carbon Co., SW of Red Lodge, For. Rd.-421, Limber Pine Campground, *S* & *Xg* 10235. Wyoming: Johnson Co., US-16, Powder River Pass, *S* & *Xg* 10213, *S* & *Xg* 10217; Park Co., US-212 E of Beartooth Pass, Beartooth Loop, above Gardner L., *S* & *Xg* 10226; US-212 2 km E of Long Lake, *S* & *Zh* 10425. — $2n = 32$. Nevada: Elko

Co., Ruby Mts., E of NV-227, Soldier Creek Trail, end of jeep trail, by creek, *S*, *Su* & *Ah* 9269; upper-mid el., edge of creek, *S*, *Su* & *Ah* 9281. — $2n = 48$. Idaho: Custer Co., SE of Chilly, Trail Creek Rd. at Big Falls Creek Rd., 41.5 km (by rd.) SW of US-93, *S* & *Xg* 10253. Montana: Carbon Co., SW of Red Lodge, For. Rd.-421, Limber Pine Campground, *S* & *Xg* 10236. — $2n = 64$. Oregon: Lake Co., OR-140 6.1 km W of Adel, along river, *S*, *Su* & *Ah* 9293. Washington: Whatcom Co., Mt. Baker, Ptarmigan Ridge Trail, *S* & *Xg* 10292. Wyoming: Johnson Co., E of Powder River Pass, Middle Fork Clear Creek Campground, along creek, *S* & *Xg* 10208. — $2n = 80$. Montana: Broadwater Co., E of Townsend, Belt Mts., For. Rd.-423, *S* & *Xg* 10325. Wyoming: Carbon Co., S of Arlington, ca. 2.3 km S of I-80, Rocky Creek Trail, *S*, *Su* & *Ah* 9206.

S. laeve (L.) Löve & Löve var. *laeve* [*Aster laevis* L. var. *laevis*]. — $2n = 48$. CANADA. Alberta: AB-43 E of Grand Prairie, W of Bezeason, *S* & *S* 10611; Jasper Nat'l. Park, Waterfowl Lake, overflow campground, *Emery* & *Emery* 1. U.S.A. Montana: Powell Co., MT-200 17.7 km W of Lincoln, *S* & *Xg* 10313.

S. lanceolatum (Willd.) G. L. Nesom subsp. *hesperium* (A. Gray) G. L. Nesom [*Aster lanceolatus* Willd. subsp. *hesperius* (A. Gray) Semple & Chmiel.]. — $2n = 64$. CANADA. Alberta: AB-43 E of Grand Prairie, W of Bezeason, *S* & *S* 10610. U.S.A. Arizona: Coconino Co., US-89 just S of Pine Flat Campground, *S* & *Ch* 9012. California: Inyo Co., US-395, N end of Big Pine, *S* & *Hd* 8671; Mono Co., Topaz, ditch by US-395, *S* & *Ch* 8906. Wyoming: Crook Co., W of center of Moorcroft, I-90 bus., *S* & *Xg* 10194. — $2n = 64 +$ ca. 6 small supernumeraries. Wyoming: Johnson Co., N of Buffalo, S of Lake Smet (T52N R82W S28), *S* & *Xg* 10199.

S. lanceolatum subsp. *hesperium* $\times$ var. *lanceolatum*. — $2n = 48-56$ (aneuploid variation on $7x$). CANADA. Manitoba: Otterburne, near Rat River, *S* 10646.

S. lanceolatum (Willd.) G. L. Nesom var. *lanceolatum* [*Aster lanceolatus* Willd. subsp. *lanceolatus* var. *lanceolatus*]. — $2n = 64$. U.S.A. South Dakota: McCook Co., Montrose, SD-38, *S* & *Xg* 10185.

S. puniceum (L.) Löve & Löve [*Aster puniceus* L.]. — $2n = 16$. CANADA. Alberta. Just S of Little Smoky, *S* & *S* 10606.

S. spathulatum (Lindl.) G. L. Nesom [*Aster spathulatum* Lindl.; *A. occidentalis* (Nutt.) Torr. & A. Gray]. — $2n = 16$. U.S.A. Oregon: OR-242 W of McKenzie Pass, vic. of Craig Lake, *S* & *Xg* 10261. — $2n = 64$. Montana: Missoula Co., NE of Lolo Pass, Lee Creek, S of Lolo Hot Springs, *S* & *Xg* 10310.

S. yukonense (Cronquist) G. L. Nesom [*Aster yukonensis* Cronquist]. — $2n = 10$. CANADA. Yukon Territory: S end of Kluane Lake, *S* & *S* 10624.

Townsendia parryi D. C. Eaton. — $2n = 36$. U.S.A. Montana: Gallatin Co. For. Rd. 6.2 km W of MT-86, W of Wilsall, *S* & *Xg* 10240.

NEW ENGLAND NOTE

AN UNUSUAL POPULATION OF
PODOSTEMUM CERATOPHYLLUM
(PODOSTEMACEAE) IN A TIDAL CONNECTICUT RIVER

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Podostemum ceratophyllum Michx. (riverweed, threadfoot) is unique ecologically and the only temperate North American species in the overwhelmingly tropical Podostemaceae. Distributed from Nova Scotia south to Arkansas and Louisiana with disjunct populations in Honduras and the Dominican Republic (Philbrick and Crow 1983), *P. ceratophyllum* occurs sparsely in the northern extent of its range. It appears on rare and endangered plant lists in all New England states except New Hampshire (Crow et al. 1981). In Connecticut, *P. ceratophyllum* has been collected from approximately 25 locations, but a number of historical populations have not persisted, including a Killingworth (Middlesex Co.) site that represented the first collection in New England.

On July 20, 2000, while surveying submerged angiosperms in tidal wetlands in the lower Connecticut River drainage, a new population of *Podostemum ceratophyllum* was found in Eight-Mile River in the town of Lyme, Connecticut. Subsequent investigation during August and early September showed that the bright green plants covered the rocks on the bottom of the river almost without interruption for a distance of more than 50 m, creating a patch of plants with a maximum width of 7 m. Upstream and downstream from this area, *P. ceratophyllum* grew abundantly over a total distance of approximately 100 m. The species occurred in scattered patches for a distance of 1.5 km upstream from this population, growing abundantly in several small areas of rapids or rapidly flowing water.

The area where *Podostemum ceratophyllum* grew most luxuriantly was freshwater, though subject to tidal fluctuation that greatly affected water depth and the strength of the current. Water depth through the area of dense growth was 10–30 cm at low tide on August 24, 2000. Current throughout this area was mea-

sured at 3.8–4.2 feet per second (fps) using a Global Water Flow Probe (Global Water Instrumentation, Gold River, CA). Plants at the downstream end of the population were under approximately 140 cm of water at high tide, and those at the upstream end were under 80–90 cm of water. Current at high tide dropped to 0.1–0.4 fps. Flow in the river declined during the next week, and current at low tide was recorded on August 31, 2000, at 1.9–3.4 fps in the area of luxuriant growth. No current was detectable at high tide. Other conditions also varied somewhat as a result of tidal influence. In the area of luxuriant growth, temperature increased from 21.4°C to 24.9°C between low tide and high tide on August 31, and turbidity declined from 2.2 to 0.8 Nephelometric Turbidity Units (NTUs).

Riverweed did not occur in upstream areas where current of less than 2.8 fps was recorded on August 24, 2000. The species occurred most abundantly in areas with current of 3.5–4.1 fps. Other conditions varied little between areas where *Podostemum ceratophyllum* grew profusely and where it occurred only sparsely or not at all (conductivity of 70–80 μ S, pH of 6.8–6.9, temperature of 19.2–19.4°C, turbidity of 1.6–1.8 NTUs). The rocky substrate appeared uniformly suitable, and significant variation in light availability was not immediately apparent: tall trees grew along both sides of the river, and no part of the riverbed received full sun throughout the day. Salinity was not measured but is not believed to be a factor in this area. In 1994, the Nature Conservancy tested for salinity downstream from this population in Hamburg Cove, which is a 3.5 km-long cove on the Connecticut River, 11.5 km north of Long Island Sound. Water within 800 m of this population was found to be free of salinity, and salinity at the nearest location where it was recorded was measured at only 2‰ (Barrett et al. 1997).

Podostemum ceratophyllum usually is associated with rapids and waterfalls, but our observations indicate that the species can grow luxuriantly in swiftly flowing water even if it is not particularly turbulent. Further, intermittent rapid flow apparently is adequate to support a large, healthy population of riverweed. Plants in the Eight-Mile River population grew luxuriantly where rapid flow occurred only during low water and where there was no current at high water. Plants were less vigorous in upstream areas beyond the reach of tidal flooding, where the current had an invariant but intermediate rate. This observation indicates that there

is a threshold water current value (perhaps near 2.8 fps) below which *P. ceratophyllum* does not occur in the river.

Tidal flux also affects flowering of the plants. Riverweed flowers only when water level drops and plants are exposed to the air (Philbrick and Crow 1992). Few plants in the Eight-Mile River population were observed in flower during August and September, 2000. Flowering plants occurred only along the margins of the river and on boulders in mid-stream that were exposed at low tide. This indicates that permanent exposure is not necessary to induce flowering in riverweed at this site. Summer rainfall was greater than usual in Connecticut, and a larger proportion of this population may flower during drier summers.

The size of this population indicates that it is neither new nor ephemeral. *Podostemum ceratophyllum* has been known to exist in Devil's Hopyard State Park (10 km upstream on the Eight-Mile River) since 1933 and was confirmed to persist on scattered rocks in rapids at that location in August, 2000. The Devil's Hopyard plants are the likely source of propagules that have colonized the river downstream. The Eight-Mile River populations are the only ones known from the Connecticut River drainage basin in Connecticut. Throughout New England, the species is known from two locations on the Connecticut River itself and from seven other tributaries—four in Massachusetts and one in Vermont, (C. T. Philbrick, pers. comm.).

Existence of this large, healthy population on the Eight-Mile River is reassuring from a conservation standpoint. Intrapopulation genetic variation among *Podostemum ceratophyllum* in the glaciated Northeast is virtually non-existent (Philbrick and Crow 1992), so each population represents an important component of the species' total genetic variability, and identification and protection of new populations becomes particularly important. However, these observations also show that there is much yet to be learned about riverweed ecology. Although the species is known to be vulnerable to chemical pollution, sedimentation, and changes in water flow (Philbrick and Crow 1983), very little ecological study of its environmental characteristics has been done (Quiroz F. et al. 1997). *Podostemum ceratophyllum* has not previously been reported from tidal waters, although a Brazilian species of *Podostemum* also is known to occur in areas that are tidally influenced (C. T. Philbrick, pers. comm.). Improved understanding of the species' ecology has importance outside the realm of bot-

any. Riverweed is the dominant macrophyte in some streams, providing structure for the invertebrate community (Everitt and Burkholder 1991). It also is an indicator species for habitat critical for the survival of several federally endangered species including the amber darter (*Percina antesella*) and the Conasauga logperch (*Percina jenkinsi*; U.S. Fish and Wildlife Service 1985). The discovery of this large population of riverweed in an area where it would not previously have been expected indicates that it may be fruitful to seek other new populations in similar, tidally influenced areas.

Podostemum ceratophyllum Michx. Connecticut: New London Co., Lyme, Eight-Mile River, N side of Joshuatown Rd. 40 m E of Old Hamburg Rd. and 240 m W of Rte 156, 20 Jul 2000, *Capers* 234 (CONN); 31 Jul 2000, *Capers* 235 & *Les* 671 (CONN).

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NEW ENGLAND NOTE

THE FIRST RECORD OF *POPULUS HETEROPHYLLA*
(SWAMP COTTONWOOD, SALICACEAE)
IN MASSACHUSETTS

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Populus heterophylla L. Massachusetts: Hampshire Co., South Hadley, on W side of Lithia Springs Rd., 0.4 km N of intersection with Elmer Brook, seasonally flooded wetland, 1 Sep 1999 and 13 Jun 2000, *Searcy s.n.* (MASS, NEBC).

While doing a survey of wetlands on the south side of the Holyoke Range, South Hadley, Massachusetts, we discovered a population of *Populus heterophylla*, swamp cottonwood. *Populus heterophylla* is a plant of the coastal plain province and is most common in the South Atlantic and Gulf regions (Godfrey 1988; Sargent 1896). It extends north up the Mississippi and becomes rare in Michigan and Ohio (Kartesz and Meacham 1999). It is also rare in the northeast, occurring as isolated populations in New Jersey, New York (Long Island), Connecticut, and Rhode Island (Kartesz and Meacham 1999). The population in South Hadley is the first location reported for the species in Massachusetts. Surveys of a large fraction of the swamps and vernal pools in the Holyoke Range have not turned up additional populations. The nearest populations of *P. heterophylla* are in Southington and Middletown, Connecticut (Graves et al. 1910), at least 50 miles to the south.

The population was growing within and along the margin of a seasonally flooded depression (probably a vernal pool) about 100 m long and 50 m wide within a larger wetland. The wetland is on Maybid silt loam, which is a deep, poorly drained soil found on old lake beds where the water table is close to the surface (Swenson 1981). The site is adjacent to a dirt road, has a few scattered cut stumps, and supports non-native invasive plants such as *Berberis thunbergii* DC. and *Rosa multiflora* Thunb. along the road margin. In addition, there is one indi-

vidual of *Catalpa speciosa* Warder, a species that naturalizes in wetlands in western Massachusetts (Burk and Prabhu 1988). However, most of the associated trees and shrubs are typical of the other vernal pools in the Holyoke Range and include *Acer rubrum* L., *Carpinus caroliniana* Walter, *Cephalanthus occidentalis* L., *Cornus amomum* Miller, *Fraxinus americana* L., *Ilex verticillata* (L.) A. Gray, *Lindera benzoin* (L.) Blume, *Nyssa sylvatica* Marshall, and *Quercus bicolor* Willd. This particular wetland also supports *Acer saccharinum* L., *Fraxinus pennsylvanica* Marshall, and *Quercus palustris* Muenchh., which are more typically floodplain species (Kearsley 1999), and some herbaceous species such as *Bidens discoidea* (Torr. & A. Gray) Britton, *Glyceria septentrionalis* A. Hitchc., and *Sium suave* Walter that are found only in a few other wetlands in the Holyoke Range.

The location in South Hadley appears to be typical of the habitat reported for the species. It is usually found along the borders of streams and swamps, and often in areas that are inundated year-round (Brown 1922; Sargent 1896). Although the South Hadley area with *Populus heterophylla* was dry in early September 1999, it was filled with water at least a meter deep several weeks later, and retained water throughout the summer of 2000. It is probably flooded most summers since other vernal pools in the area with a similar flora retain water most of the summer. Several of the populations of *P. heterophylla* in Connecticut also occur in swamps or along the Connecticut River, but there is one extant population in the state reported from a vernal pool near the summit of a traprock ridge (Mehrhoff 1989).

Populus heterophylla was one of the dominant trees at the South Hadley site and showed evidence of extensive vegetative growth. There were at least 24 stems of tree size (DBH > 10 cm), 77 stems in the sapling range (DBH 4–10 cm), and several hundred shoots with a diameter of 1 cm or less. The largest tree had a diameter at breast height (DBH) of 36 cm, which is about the size listed for mature trees of this species in New York (Brown 1922).

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NOTE

UTRICULARIA MYRIOCISTA (LENTIBULARIACEAE)
IN COSTA RICA: A NEW RECORD
FOR CENTRAL AMERICA

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In a taxonomic treatment of the genus *Utricularia* (Lentibulariaceae) in Costa Rica (Crow 1992) I reported a total of 10 species, including a purple-flowered submersed species with whorled branches discovered in 1984 and determined by me as *U. purpurea* Walter. The species was represented in Costa Rica from only a single population in a small pond at Buenos Aires in the southern region of the country. At the time I was aware of only a single, North American species having whorled leaves and purple flowers (Crow and Hellquist 1985), and a range extension from Veracruz, Mexico, and Belize to Costa Rica did not seem unreasonable. Taylor's annotation of the specimens at the Missouri Botanical Garden (MO) concurred with the identity as *U. purpurea* and he included Costa Rica in the range of the species in his monograph of the genus (Taylor 1989).

Subsequent research in wetlands in Bolivia revealed an additional submersed *Utricularia* with purple flowers and whorled leaves that was ultimately identified as *U. myriocista* A. St. -Hil. & Girard. An additional visit to the Buenos Aires population, and comparison with material of *U. purpurea* from New Hampshire [Ritter 4821 (NHA), Crow 9845 (NHA)] and *U. myriocista* from Bolivia [Ritter, Crow, Garvizu & Solíz 4394 (MO, NHA, USZ)], has resulted in a redetermination of the Costa Rican population as *U. myriocista*. Examination of specimens from Belize [Schipp 6006 (F) and Pelly 41 (F)] confirmed that Taylor's (1989) report of *U. purpurea* in that country is correct.

Previously known only from South America, *Utricularia myriocista* is widely distributed in tropical lowlands from Venezuela, Guyana, Surinam, and French Guiana south through Brazil to the lowlands of adjacent northeastern Argentina (Corrientes) and eastern Bolivia (Ritter and Crow 2000; Taylor 1989). Thus, this

represents the first report of *U. myriocista* for Central America as well as Costa Rica.

As noted by Taylor (1989) the differences between the South American *Utricularia myriocista* (Figure 1a, b, c) and North American *U. purpurea* (Figure 1d, e) are small. Both species belong to *Utricularia* L. sect. *Vesiculina* (Raf.) P. Taylor, along with a third, very similar South American taxon, *U. cucullata* A. St. -Hil. & Girard (Venezuela to Brazil; Taylor 1989). All three taxa are submersed aquatic plants with bladder-bearing leaves in whorls of 4–5, the primary segments bearing additional whorls further divided into whorled or opposite capillary segments, with terminal bladders (traps). All have flowers borne solitary or in few-flowered racemes (typically with one flower open at a time), with the corolla light purple to rose-pink; the lower lip 3-lobed with 2 lateral lobes conspicuously saccate. Table 1 compares the distinctive features of the two closely related South American species with the North American taxon. The most distinctive features distinguishing the *U. myriocista* and *U. purpurea* involve the spur, the shape of the lower lip of the corolla, and the attachment of the bracts.

The site of the Costa Rican collection, on the outskirts of Buenos Aires, is a shallow pond less than 1 ha in size, bordered by the road into town as well as several shanties (whose sewage drains to the pond), and is adjacent to a large pineapple field. Once a savanna-like region in the Valle de El General south of San Isidro, the area is now mostly pineapple fields. A second small laguna lies less than 100 m to the north and historical herbarium records of various species from this vicinity suggest that this area may have been dotted with lagunas in the past (Crow 1993).

Based on several visits to the Buenos Aires laguna over the past 16 years, my catalog of the aquatic flora lists 35 species in 17 families (G. E. Crow, unpubl. data). While the diversity may not appear high, this laguna has a rich assemblage of aquatic plants not seen by the author elsewhere in Costa Rica (Crow 1993). In addition to being noteworthy for a new record for *Utricularia myriocista* in both Costa Rica and Central America, the laguna is also home to several other species of *Utricularia*: *U. gibba* L. (common, widely distributed), *U. hydrocarpa* Vahl, another purple-flowered species, often growing mixed with *U. myriocista* (known from only a few localities in Costa Rica), and



Figure 1. Distinctive features of *Utricularia myriocista* and *U. purpurea* [Crow 9845 (NHA)]. a. *U. myriocista* habit of showing whorled arrangement of leaves [Crow 9682 (NHA)]. b–c. *U. myriocista* flower, showing slender spur with acute apex (arrows) [Crow 9617 (NHA)]. d. *U. purpurea* flower, spur hidden by strongly involute margins of midlobe of lower lip. e. *U. purpurea* flower, view from below showing short-conical spur with obtuse apex (arrow), lying beneath notched lower midlobe.

Table 1. Summary of distinctive comparative features of the taxa of *Utricularia* section *Vesiculina* (adapted primarily from Taylor 1989).

Character	<i>U. purpurea</i>	<i>U. myriocista</i>	<i>U. cucullata</i>
Flowers	1–3	1–5	1–2
Corolla	0.8–1.8 cm long	1–1.7 (–3) cm long	0.4–1.5 cm long
Upper Lip	Nearly circular with apex rounded, broad shallow notch at apex	Nearly circular with apex rounded	Ovate-oblong, with apex rounded, truncate or slightly notched
Lower Lip	Midlobe quadrate (appearing narrowly quadrangular due to strongly revolute margins), the apex truncate and usually notched up to 0.5 mm	Midlobe narrowly ovate, the apex rounded	Midlobe oblong, the apex rounded to subacute
Markings	Yellow spot at base of lower lip in throat of corolla	Yellow spot at base of lower lip in throat of corolla	2 white or yellow spots at base of lower lip in throat of corolla
Spur	Short-conical, apex obtuse; distinctly shorter than lower lip, usually half as long; spur hidden by midlobe	Slender, slightly curved, tapering to acute apex; 2/3 to slightly exceeding the lower lip; spur not hidden by midlobe	Subulate straight or slightly curved, apex subacute or shortly bifid; usually conspicuously exceeding the lower lip; spur not hidden by midlobe
Pedicel Bract	Medifixed (pelate)	Mostly basifixed	More or less medifixed or spurred

U. pusilla Vahl (few sites in the country). Furthermore, several other species in the pond are known only in Costa Rica from this single locality, including *Benjaminia reflexa* (Benth.) D'Arcy, *Eriocaulon schippii* Standl. ex Moldenke, *Ludwigia torulosa* (Arnott) H. Hara, and *Sagittaria rhombifolia* Cham. [the latter of which was initially misidentified and described as a new species, *Echinodorus botanicorum* L. D. Gómez & Gómez-Laur. (1982), with this laguna as the type locality]. Two other species are known only from a few sites in Costa Rica: *Luziola fragilis* Swallen and *Xyris laxifolia* Mart.

This area has long experienced agricultural impacts. However, a new threat may come in the form of flooding upstream from a huge new proposed hydroelectric dam and reservoir project on the Río Grande de Térraba. Although the full extent of flooding has not been determined, according to the newspaper *La Nación* (Ramírez 2000), the area around Buenos Aires is expected to be heavily impacted. Thus, noteworthy as an aquatic site with such a rich assemblage of unique plants, the laguna at Buenos Aires is certainly a locality that should be a high priority for conservation.

Utricularia myriocista A. St. -Hil. & Girard. COSTA RICA. Prov. Puntarenas: Buenos Aires, shallow pond, 9°10'N, 83°20'W, 9 Nov 1984, *Crow* 6175 (CR, F, MO, NHA); 23 Nov 1984, *Crow* 6254 (CR, NHA); 4 Aug 1987, *Crow* 6971 (CR, F, MO, NHA); 18 Aug 1999, *Crow* 9617 (CR, INBIO, MO, NHA); 2 Oct 1999, *Crow* 9682 (CR, INBIO, MO, NHA); laguna, 5 Sep 1984, *Gómez* 24014 (MO); 14 Sep 1985, *Grayum & Herrera* 6066 (MO).

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BOOK REVIEW

Synthesis of the North American Flora, Version 1.0 by J. T. Kartesz and C. A. Meacham. ©1999. CD-ROM interactive software. ISBN 1-889065-05-6 \$495.00. MS Windows 3.1, NT, 95, 98 or 2000 operating system. Minimum system requirements: Pentium 90 MHz-class processor, 32 MB RAM, 25 MB free hard drive space, SVGA display (800 by 600 pixel resolution) with 16 colors. Available from the publisher: North Carolina Botanical Garden, University of North Carolina at Chapel Hill, CB #3375, Totten Center, Chapel Hill, NC 27599-3375.

Botanists working with the vascular flora of North America have long needed a comprehensive, authoritative source of names of vascular plants and their synonyms coupled with information on their geography, common names, biological attributes, and uses. This publication on CD-ROM comes very close to filling that need. The amount and quality of the data included in the *Synthesis*, and its ease of use, are very impressive.

The purpose of the *Synthesis* is to “produce an accurate and comprehensive database on the taxonomy, nomenclature, phyto-geography, and biological attributes of North American vascular flora in combination with an effective software program for accessing the database.” John Kartesz has created the database and Chris Meacham the software; both have done exceedingly well. The scope of the project is so grand that one could be forgiven for being skeptical about its comprehensiveness, accuracy, and effectiveness. But after using it for some months in connection with editing the Orchidales for *Flora of North America*, I am very favorably impressed by its completeness and by how easy it is to use.

The *Synthesis* actually began with the two checklists of the vascular flora of North America written by John Kartesz (Kartesz 1994; Kartesz and Kartesz 1990). The geographical scope of the *Synthesis* has been expanded to include North America north of Mexico (including the continental United States, Canada, the French islands of St. Pierre and Miquelon, and Greenland), as well as Hawaii and the Caribbean islands of Puerto Rico and the U.S. Virgin Islands. The taxonomy in the earlier checklists has been revised and now includes 22,006 accepted species. Obvi-

ously the author could not be a specialist on all members of this flora, but he has effectively relied on published literature and on the counsel of a large group of taxonomists who have either reviewed his work or provided original contributions. The taxonomy presented reflects, in addition to the author's insights and decisions, the most recently published studies as well as the opinions of specialists. The synonymy, which probably includes well over 300,000 names, permits the user to find most names that have been used in our flora; even some as yet unpublished names have been included. It is unfortunate, however, that the basis for the taxonomy is not referenced because it would be useful to know whose opinion is being followed. The nearest one can come to determining the authority for a particular taxonomy, therefore, is to check the list of "taxonomic, nomenclatural, and/or phyto-geographic data contributors and reviewers" and to infer what input the listed authorities may have had.

Information on the distribution of about 28,000 taxa is given to the state level or its equivalent. For most occurrences some form of documentation is available. For example, when a map is displayed and the cursor is placed on a state or province, a fly-over window displays the documentation. Sometimes this may cite a published flora or monographic study, a reference to a Natural Heritage Program report, or a voucher specimen in an herbarium. Sometimes it simply states "present." A random sample of 50 taxa showed that documentation was provided for about two-thirds of them. In some families, for example the Poaceae, no documentation is provided. This means that user satisfaction will vary depending on the group being queried. In addition to documentation, the states in which a taxon occurs are color-coded to indicate whether it is present, rare, extirpated, or extinct. An interesting feature is the use of cross-hatching to indicate that a taxon's occurrence there is questionable. The inclusion of even unlikely reports will be very useful to the monographer who may wish to follow up every lead. Lists of the phytogeographical literature and periodicals consulted are provided.

The *Synthesis* includes information for each taxon under the headings: major plant group, habit, duration, nativity, weeds and invasive plants, habitat, morphology, trophic level, rarity and endemism, human use plants, toxicity, Native American medicinal uses, plants that attract, and U.S. federal lands. This part of the database is not as complete as those on nomenclature and phy-

to geography. Much of the information seems to have been developed in connection with specific contracts, usually from U.S. federal agencies, and the information is not complete for the entire flora area. Exceptions are rarity and endemism, for which extensive use was made of reports from the Nature Conservancy, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), and the Canadian rare plants project. Information on Native American medicinal use also is relatively complete inasmuch as it incorporates a two-volume work on the subject (Moerman 1986). But, for example, only a few habitat types are included and no mention is made of weediness in Canada. The section dealing with biological attributes is an interesting addition to the database but is not its major strength.

I found the software to be relatively intuitive to use, and when I was confronted with problems the documentation was thorough and clearly presented. The windows are well arranged and can be easily customized. It is very easy to perform the basic operations of listing taxa in various ways and to relate names to geography. The software also facilitates questioning the data and combining name, geography, and biological attributes in a variety of ways. One can, for example, list all members of a genus for a single state or group of states, or list all taxa for one or more states and provinces. The lists may comprise only accepted scientific names, with or without authority, or may include synonyms (which may be arranged in thesaurus or checklist format) or common names. One can create lists of woody plants, aquatic plants, exotic plants, toxic plants—you name it. The taxonomic and geographic information then can be combined with biological information, for example: all woody taxa used by Native Americans in Ontario. In all cases the lists created can be saved as a file.

From my point of view, the most important shortcoming of the *Synthesis* is that the phytogeographical data are given only to the state/province/territory level. This is a serious problem in western United States, Alaska, and Canada where state-level units are very large and the generalized coloring of these areas does not provide much understanding of distribution. I have been told, however, that the database is now being supplemented with county-level data, where it is available; that will enhance the display of distribution patterns for many regions but it will not do much for northern or western Canada or Alaska, where county-level

subdivisions are lacking. It should be noted, however, that while distribution for the Northwest Territories is displayed by the general coloring of the entire territory, the occurrence of species on each of the islands in the Canadian Arctic Archipelago is documented separately; the new territory of Nunavut is not included. The authors are presently working on the completion of documentation. Even when it is done, however, problems will remain in assessing the distribution of taxa whose circumscriptions have been changed by taxonomic study, or in verifying the identification of range extensions.

Plans for future updates are almost as ambitious as the *Synthesis* itself. It is proposed that future editions will include information on introductions, degree of invasiveness, national endemism, a U.S. national rare plant list, illustrations, expanded morphological categories, a random access (polyclave) key, and much, much more.

Finally, a concern that I would have before purchasing the *Synthesis* is its cost. If purchased directly from the North Carolina Botanical Garden, the price is U.S. \$495.00 plus shipping (Canadian \$756.00; all sales should include two free upgrades). While I am sure this represents its true value, not many individual botanists will be willing or able to pay this price. However, libraries, governmental agencies, and consulting firms will find it a bargain, for the *Synthesis* is a gold mine of information.

The *Synthesis* is not only a completely synonymized, searchable checklist of the flora of North America, but it can be used to create checklists to suit any need. What is more, the list of accepted names is constantly being revised as new taxonomic studies are published or as volumes of the *Flora of North America* appear in print. In that respect it should be noted that the *Synthesis* is not a substitute for *Flora of North America*, but rather a helpful companion to it. The *Synthesis* does not have keys to genera and species, descriptions, bibliographic citations for names and basionyms, outline maps, or discussion of taxonomic problems; but it does permit the manipulation of names and the linking of information to those names in ways that a hard-copy flora cannot.

For years there has been talk of computerizing taxonomic information. John Kartesz and Chris Meacham, with help from a host of collaborators, have slowly and methodically been doing something about it. The *Synthesis* presents the botanical com-

munity with a very useful, modern botanical tool that integrates nomenclatural, phytogeographic, and biological information in a way that once could only be dreamed about.

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NEBC MEETING NEWS

December 2000. Paul Somers introduced the evening's speaker, Dr. Maile Neel, currently working as a Visiting Investigator at the Marine Biological Laboratory in Woods Hole and a Postdoctoral Researcher in the Department of Botany and Plant Sciences at the University of California, Riverside. Maile is also working on the mysteries of the sandplain *Gerardia* (*Agalinis acuta*) with her colleagues in Massachusetts. "The structure of diversity: Implications for reserve design" was the focus of her doctoral and postdoctoral studies and her topic for this evening's presentation.

Maile said she is interested in preserving ecosystem composition, structure, and function, and in the consequences of using different approaches to meet this goal. Land managers can focus their conservation efforts on individual rare species, overall species diversity (i.e., species richness "hotspots"), or community diversity. Dr. Neel's research centered on the question: how well does research focusing on one of these levels of diversity serve to simultaneously conserve other levels of diversity?

Maile's work was conducted in the San Bernardino Mountains of southern California. These mountains are good candidates for such an investigation because they support a high level of plant endemism (~40 species), have a high level of plant and vegetation community diversity in general, and are under constant pressure for surface and near-surface mineral extraction. The Mining Law of 1872 allows access to mineral resources on federal land, and 90% of the National Forest land in the San Bernardino Mountains is under claim by limestone mining companies. A handful of endemic species is at risk of extirpation, including *Astragalus albens*, *Erigeron parishii*, *Eriogonum ovalifolium* var. *vineum*, *Lesquerella kingii* subsp. *bernardina*, and *Oxytheca parishii* var. *goodmaniana*. Because of habitat loss and degradation as well as the risk of future losses, these species were listed under the Endangered Species Act. The U.S. Forest Service, U.S. Fish and Wildlife Service, and others are interested in developing a conservation plan that will identify sites to be protected from mining to ensure the persistence of these taxa and the habitats on which they depend.

Maile set about her fieldwork by establishing 669 sampling plots, including 250 on carbonate soils, 245 on non-carbonate soils, and 174 with known populations of the species in question.

Data collected helped to elucidate the composition of plant communities, species richness, and the distribution of endemics, as well as genetic diversity (by the investigation of isozymes). Standard ecological parameters were measured at every plot, including slope, aspect, elevation, and soil characteristics (pH, % Ca, and % Mg). Isozyme sampling was conducted on subsets of the plots, and included four species: *Astragalus albens*, *Erigeron parishii*, *Eriogonum ovalifolium* var. *vineum*, and *Oxytheca parishii* var. *goodmaniana*.

The data support a picture of composition that includes 13 vegetation types, 8 of those widespread. Elevation plays a key role in distinguishing the sample plots, although slope angle, outcrop, % Ca, and % litter are not far behind, as revealed by canonical correspondence analysis. Of the 502 taxa, 90% were identified in 90 or fewer of the nearly 700 plots. Species richness increases with low elevation and less carbonate in soils. The results of isozyme analysis reveal the four San Bernardino endemics in question to have levels of genetic diversity that are more similar to widespread species than to typical endemics. Only *Oxytheca* displayed a percent polymorphism, number of alleles/locus, and expected heterozygosity of classic endemic species. Maile asked, "How well do areas of high species richness represent community diversity, overall species richness, and occurrences of the endemic species?" She learned that one would miss a good deal of the community diversity by focusing on richness alone. Further, species-rich plots did not include significantly more total species than the same number of plots chosen at random. The endemic plants tended to be found in sites with moderately high species richness, but not in sites with the highest richness. Maile also asked, "How much do the distributions of the endemic taxa represent the range of community diversity and how well do they overlap with one another?" When she looked just at *Erigeron parishii* or *Eriogonum ovalifolium* var. *vineum*, for example, she learned that they occupy only about half of the length of the environmental gradients represented by the canonical correspondence analysis. Not surprisingly, the endemics are biased to the carbonate soils and each taxon is limited in the elevational gradient it occupies. Further, the plants are limited in their distribution on carbonate soils, only occurring in 20% of the randomly sampled plots on these soils. In terms of overlap among the taxa, *Erigeron* and *Astragalus* have the most, sharing 97% of their

distributions along the environmental gradients, yet they are found in the same plot in less than 20% of the 669 plots. The smallest amount of overlap was between *Lesquerella kingii* subsp. *bernardina* and the other taxa; *Lesquerella* only overlapped with *Eriogonum* once and never overlapped with the other taxa. When Maile explored the relationship between total species richness and endemic plant taxa, she learned that sites supporting the endemic taxa would include fewer total species than the same number of plots chosen at random. Areas of high genetic diversity are just as difficult to predict, showing no patterns at all!

Maile concluded that ecological reserves created for one level of diversity would not necessarily capture other levels of diversity. Notably, conserving endemic taxa does not conserve community or species diversity. Community conservation approaches are likely to miss a significant portion of the species diversity and necessarily will not replace detailed species-focused conservation efforts. On the other hand, community-level efforts are more likely to conserve individual endemic taxa than single taxa efforts are likely to conserve community diversity.

January 2001. The Club's first botanical potluck preceded the meeting. There were assembled some 20 main dishes, including one rather unique quiche-like prize consisting of eggs and young milkweed inflorescences, as well as numerous snacks and dessert-like comestibles. President Lisa Standley declared it unilaterally a success. Not a soul rose to contest. Lisa reminded everyone that dessert and the usual refreshments were waiting for the conclusion of the annual members' "show & tell."

Nancy Eyster-Smith secured a variety of electronic and video projection equipment for the evening, and Don Lubin was first up with a PowerPoint perusal of the ferns upon which he has obsessed during the past many months. Of particular note, Don had digital images to show of *Dryopteris intermedia* × *marginalis* hybrids and their parents, as well as a wonderful collection of the cliff-hugging ferns of Gaspé haunts. Jenn Forman was up next with the digital projection equipment. Weeds fascinate Jenn, so it comes as no surprise that she spent free time during two visits to Italy hunting weeds. Abruzzo is a rugged place, dotted with flocks of sheep and goats. Amongst the weeds was a collection of stunning and fierce thistles. Jenn also found two species of North American *Epilobium* that have invaded Europe, an *Im-*

patiens that made the jump from the Himalayas to Italy, and a *Hibiscus* whose range has been expanded to both Europe and North America from Africa.

Russ Cohen has been exploring and teaching about edible plants for more than 20 years. He had short stories to tell of the likes of evening primrose, black locust, pokeweed, milkweed, and others. Learning to cook with corn smut and barberry provided Russ with his best stories for the evening. Hot peppers turn smut from a miserable and nearly unpalatable meal to a marvelous delicacy. A failed attempt to make barberry jelly turned into the best little pot of wine Russ has ever tasted. Lisa Standley was up next with a short tour of the flora of the southern mountains of New Zealand. Lisa has been waiting for years to see *Nothofagus* in its native clime, and she was not disappointed. The rain forests of the region are filled with tree ferns. The branches and trunks of other forest trees are festooned with bryophytes, ferns, and mushrooms, including some spectacular species of *Hymenophyllum* and the brilliant little electric-blue cap of an associated basidiomycete. Tiny *Euphrasia* plants and “vegetable sheep” (a peculiar, mat-forming, dwarf composite) are amongst the botanical treasures that visitors to Milford Sound are likely to find. The international theme continued with Tom Philbrick, who traveled from southwestern Connecticut to tell us of his latest forays to Mexico, Brazil, Paraguay, Uruguay, and Argentina in search of the Podostemaceae. There is nothing quite like *Podostemum* in full bloom growing on rocks in shallow water streams and rivers of Central and South America.

Chris Canfield was up next to bring us back to New England and a tour of a local Connecticut bog, complete with *Eriophorum*, *Drosera*, and *Sarracenia*. The vegetation is likely to change if the work of beavers continues to re-flood the bog unchecked.

Globetrotting again, Dr. Gandhi gave us a quick tour of the flora of the Hassan District of southwest India. There, within 100 miles, rainfall ranges from 15 to over 200 inches/year. The forests include both teak and sandalwood, managed carefully for centuries. Gandhi promised a full presentation at a future member meeting. Elizabeth Farnsworth of NEWFS and her husband, Aaron Ellison of Mount Holyoke College, traveled recently to the Kimberley district of Australia, where they found baobab, elephant ear, and *Bauhinia*. A tuberous *Drosera* and exotic pipe-worts grow along the banks of Mitchell Falls, which cut through

billions-of-years-old sandstones in Bell Gorge. The plants appear to be guarded by a gang of “freshies,” the Australian freshwater crocodile. Pat Swain then took us back to Iguassú Falls in Argentina, and showed us some of the more typical trees and shrubs of the towns. Pat was followed by Marsha Salett, whose recent trip to Hawaii brought her to the first, and we hope not the last, National Wildlife Refuge created for the protection of songbirds. A little closer to home, Robert Bertin caught Tom Rawinski smiling in the middle of the single largest stand on record of *Scirpus longii*. After snapping the picture, Robert headed off to the slopes of Mount Hood and Mount St. Helens, where fireweed, red alder, and lupines were thriving.

The evening concluded with images of the Club’s recent trip to the Gaspé, Quebec. Bill Cullina and George Newman captured the rare herbs and ferns with brilliant photography, and Nancy Eyster-Smith wrapped up the evening with a ten-minute video that captured botanists, family members, northern gannets, and hang-gliders enjoying this rugged, mountainous, and wet corner of our world.

—DON HUDSON, Recording Secretary.

February, 2001. Dr. Stephanie Neid of the Massachusetts NHESP’s BioMap Program discussed the results of her doctoral research at the University of Minnesota, where she studied the effects of deicing salt on the growth of inland salt marsh species. One of the objectives of her research was to identify native halophytes that could be used to stabilize roadsides along the highly salted Minnesota highways. She used greenhouse-grown plants and seeds from two disjunct populations of *Distichlis spicata* and *Puccinellia nuttalliana*, as well as the cultivated *P. distans*, to determine how increasing concentrations of salt affect germination, growth, and flowering, and to determine if there were ecotypic differences between populations. *Puccinellia distans* is least affected by high salt concentrations and has the lowest genetic variability, which account for its successful migration along highways. Both *P. nuttalliana* and *Distichlis* showed considerable variation between populations in their response to salt and in their electrophoretic isozyme patterns, indicating that ecotypic differences have evolved. Dr. Neid concluded that *P. nuttalliana* has the potential to become an important plant for roadside revege-

tation and stabilization, if artificial selection is used to identify the most salt-tolerant ecotypes and to decrease variability. *Disticlis*, due to low seed germination rates, is less suited to roadside use unless new rhizome propagation techniques are used.

—LISA A. STANDLEY, Recording Secretary *pro tempore*.

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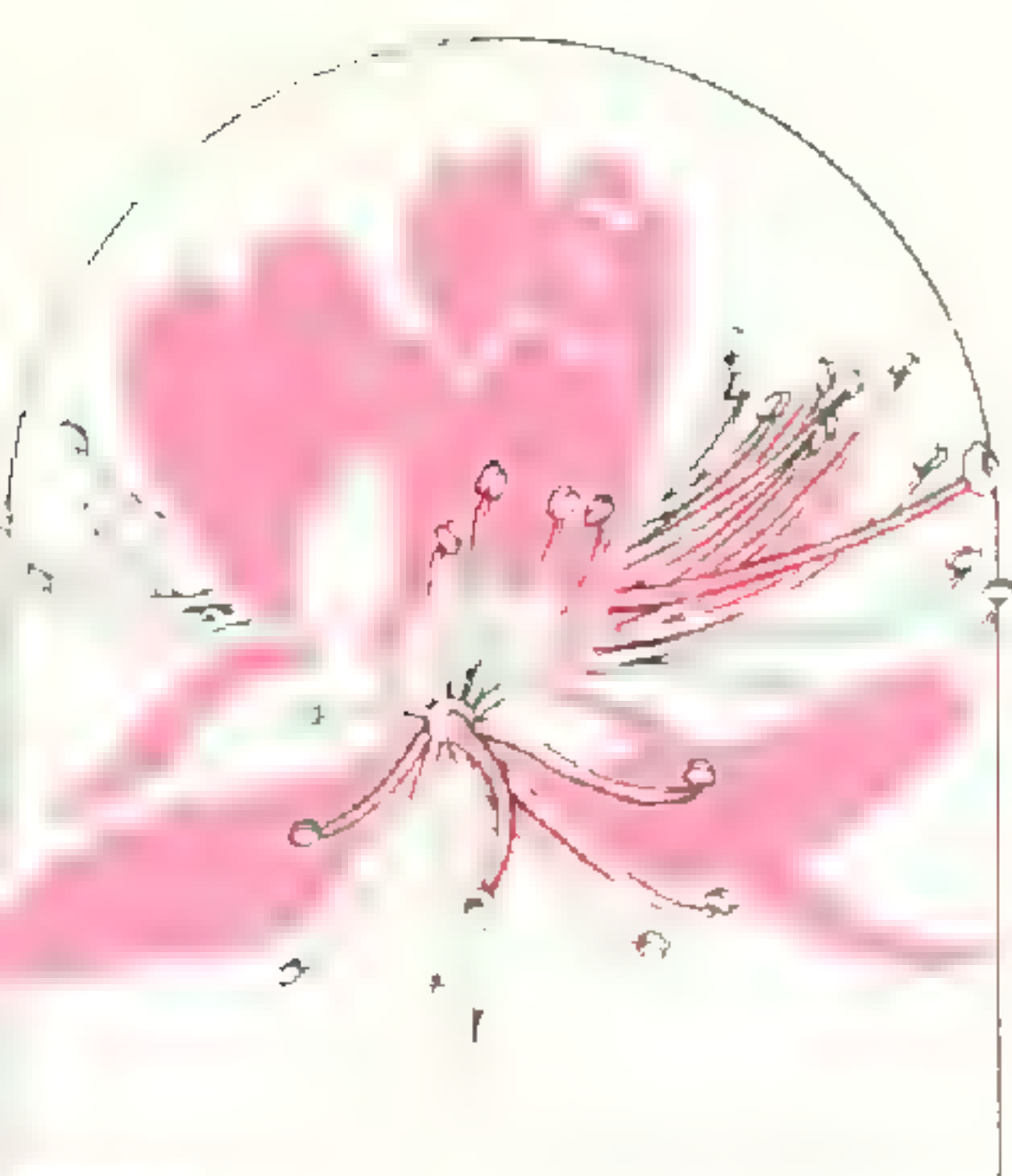
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CHECKLIST OF *SPHAGNUM* IN NEW HAMPSHIRE

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ABSTRACT. Forty-three species and two subspecies of *Sphagnum* are reported for New Hampshire, including fifteen species and one subspecies documented from herbarium records and recent collections. Diversity at county and biophysical subsection (ecoregion) levels is presented and areas that remain undercollected in the state are highlighted. New Hampshire has a great diversity of *Sphagnum* species, reflecting the diversity of climatic, geologic, and environmental characteristics of the state. Several species with restricted distributions are discussed, and habitats critical to these species are described for future conservation efforts.

Key Words: *Sphagnum*, New Hampshire

The distribution of sphagna in New Hampshire can be interpreted in terms of the particular phytogeographic and habitat affinities of each species. In general, plant species with alpine, boreal, montane, eastern deciduous forest, and coastal plain affinities are all well represented in New Hampshire (Sperduto 1996; Weatherbee and Crow 1990). Plant assemblages in the state reflect not only these broad-scale climate-driven phytogeographic affinities, but also finer scale differences in hydrologic and nutrient regimes (Sperduto 1997, 2000). Peatlands are frequent within the mosaic of upland acidic forests on till (e.g., spruce–

fir, northern hardwood, and transitional hardwood–conifer forests). The dominant peatlands are open and acidic. Despite the predominance of acidic conditions, circumneutral to calcareous communities are well represented in smaller patches, including calcareous fens and swamps. In sum, 43 wetland types have been described from New Hampshire (Sperduto 1996).

Sphagnum is found as a minor component in many of New Hampshire's wetland community types. Peat mosses achieve greatest importance and diversity in four wetland systems in the state: open bogs, open fens, forested basin swamps, and forested seepage swamps. These systems include 13 of the 43 wetland types based on characteristic vegetation and environmental conditions (Sperduto 1997, 2000). Peatland types range from alpine to coastal and from acidic to calcareous. This checklist is the first to include collection sites representing all wetland types present in the state.

Prior to the present study, D. C. Eaton and E. Faxon made the most concerted effort to document *Sphagnum* species in New Hampshire. Eaton and Faxon collected *Sphagnum* in the northern counties of Coös and Grafton in the 1880s and 1890s (Reid 1987). The results were published in two exsiccatae: North American *Sphagna* (N.A.S.) collected by E. Faxon and *Sphagna Boreali-Americana* (S.B.A.) collected by D. C. Eaton and E. Faxon. Fifty-six of the 172 numbered specimens in S.B.A. were collected in New Hampshire. William G. Farlow was also an important early collector of *Sphagnum* in the state. More recent collections include those of A. R. Hodgdon in the 1950s and 1960s from Strafford and Carroll counties and Holcombe (1979), who reported the first New Hampshire collection of *S. angermanicum* from Ethan Pond in the White Mountains.

There are only two previous lists that include New Hampshire *Sphagnum* species. The first is Sphagnaceae of New England reporting 27 species (Andrews 1906) and the second is a preliminary list of New Hampshire mosses that includes five *Sphagnum* species (Allen 1992). Together these lists report 29 species for the state. The general scarcity of collections and their concentration in the White Mountain area has resulted in a severe lack of documentation for the majority of the state.

The purposes of this paper are: 1) to present a checklist for *Sphagnum* species in New Hampshire based on herbarium specimen annotations and field collections (Appendix); 2) to discuss

currently known species distributions and habitat restrictions within the state; and 3) to highlight current and potential threats to the diverse *Sphagnum* flora of New Hampshire.

MATERIALS AND METHODS

New Hampshire spans 290 km of latitude and an elevation range from sea level to 1912 m at the summit of Mount Washington, the highest point in northeastern North America. On average, the state's climate is cool-temperate, with extreme local variation. Average annual temperatures range from 5 to 7.8°C throughout most of the state; however, the average annual temperature is -3°C on Mount Washington. July temperatures average 18.9 to 21°C while January temperatures average -5.2 to -9.1°C . Precipitation is fairly evenly distributed throughout the seasons. Total annual precipitation varies from 104 to 112 cm across most of the state, with a high of 178 cm on Mount Washington. Annual average snowfall varies from 127 cm on the coast to 165 to 178 cm inland and 470 cm on Mount Washington. Length of the growing season varies from less than 105 days in the north to 140 days in the south. Eighty-three percent of the state is still covered by forest. New Hampshire ranks 47th out of 50 states in wetland area. Ninety-three percent of the original wetland areas are still in existence (Dahl 1990).

The checklist is based on both herbarium and recently collected specimens (see Appendix). All *Sphagnum* specimens from New Hampshire located at BING, BH, and NHA were examined, as well as selected specimens from NY, FH, and YU. In addition, over 1500 collections were made by the authors from 86 wetland sites. Field collections were initiated in 1994, largely at the A. Le Roy Andrews Foray. During this foray several coastal plain wetland sites were collected including the Ponemah bog and fen system, Hampstead Atlantic white cedar swamp, Dead Pond in Pawtucketaway State Park, and Spruce Pond at Bear Brook State Park. In 1999, the A. Le Roy Andrews Foray was held again in New Hampshire and selected collections by Andrus from sites in Carroll County are included here. Through 1994 and 1995, Cleavitt conducted bryophyte surveys of the Hubbard Brook Experimental Forest (Cleavitt and Fahey 1996) and six Research Natural Areas (RNAs) within the White Mountain National Forest (Cleavitt 1996). Sperduto and Nichols collected *Sphagnum* during state-

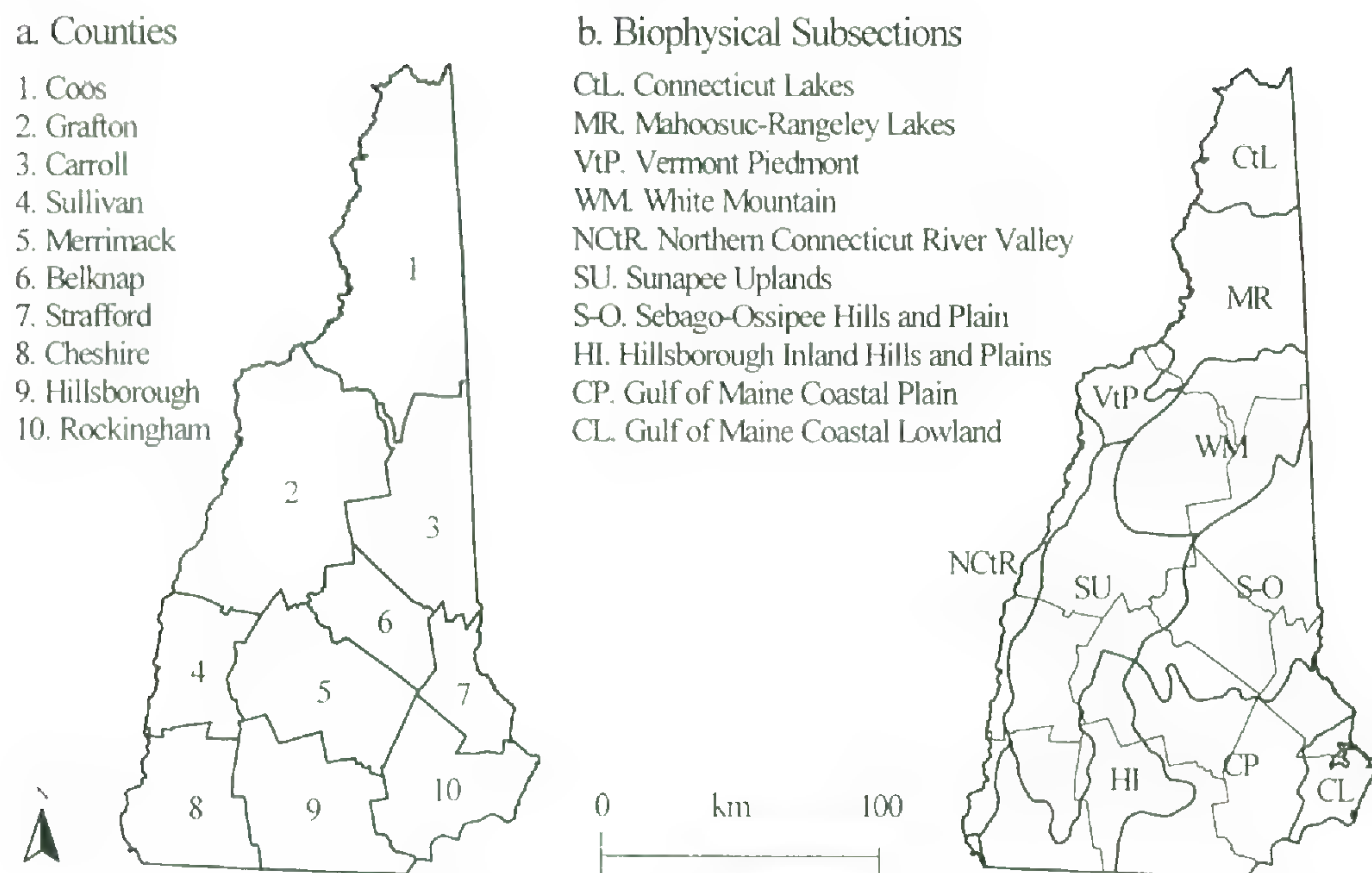


Figure 1. Maps of New Hampshire showing a. county boundaries, and b. biophysical subsections (heavy lines) in relation to county boundaries (fine lines).

wide wetland surveys during the years 1994–1998 and 1997–1998. United States Department of Agriculture Forest Service ecoregion subsections (Keys and Carpenter 1995) and vegetation units (Sperduto 1997, 2000) within the state were used to help direct field work and identify potential information gaps.

Sphagnum species are reported in a conventional manner according to county distribution (Figure 1a) and based on ten biophysical subsections (ecoregions) defined by the U.S. Forest Service (Keys and Carpenter 1995; Figure 1b). Subsections represent landscape-level units within the state that share similar assemblages of physiography, vegetation, soils, and climate, and are used here since they relate more closely to the distribution of vegetation types in the state than do politically based counties. Nomenclature follows Anderson (1990) except for *S. brevifolium* (Flatberg 1992b), *S. majus* subsp. *norvegicum* (Flatberg 1987), and *S. viride* (Crosby et al. 1999).

RESULTS

Examination of herbarium material revealed 233 unicate specimens representing 51 county and 4 state records not recorded by

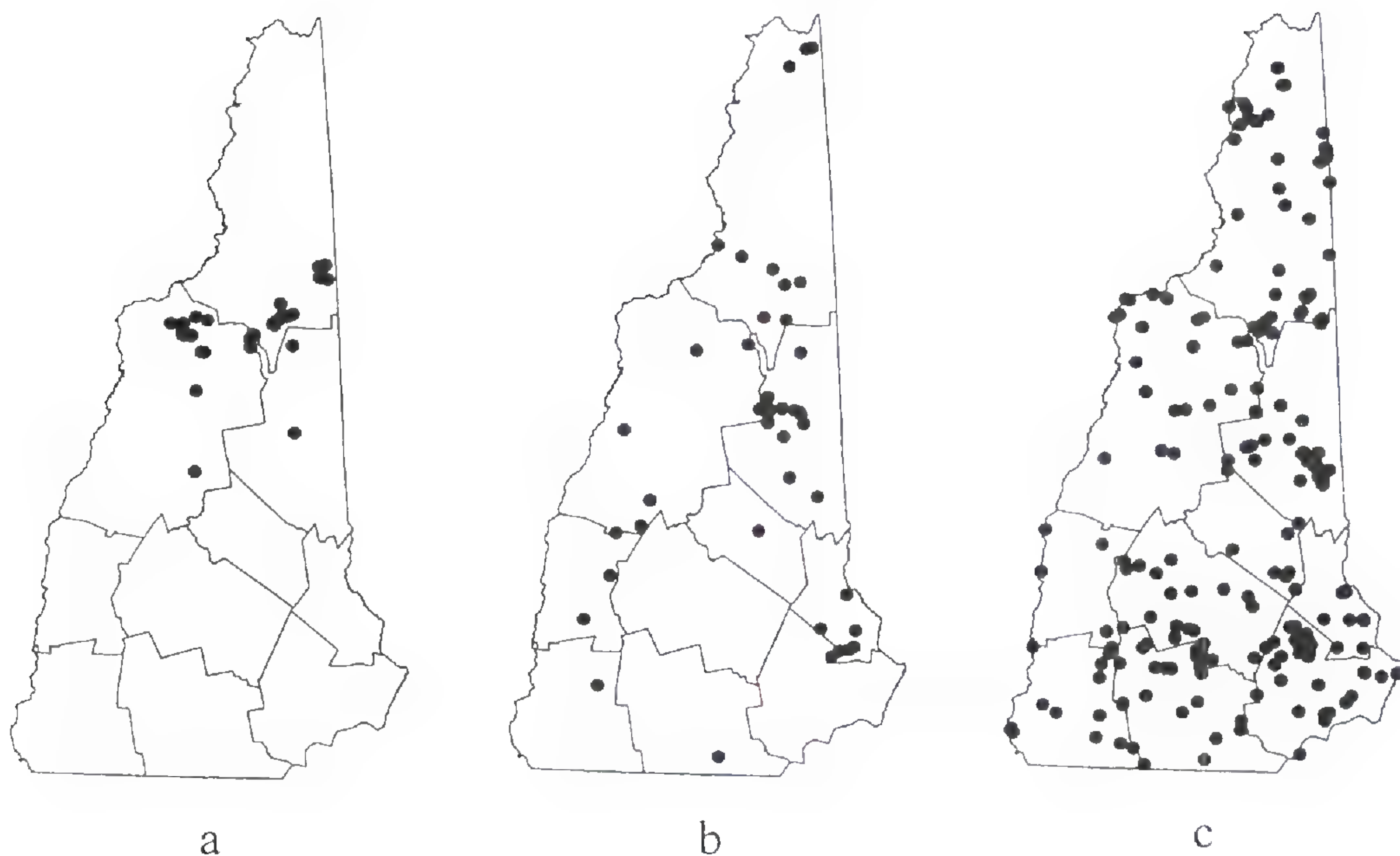


Figure 2. New Hampshire county maps depicting collection site location and intensity over time with a. pre-1900 collection sites; b. 1901–1990 collection sites; c. post 1990 collection sites (two of these sites were not collected by the authors).

Andrews (1906) or Allen (1992). Our collections further added 213 county and 11 state records. Figure 2 depicts the concentration of historical collections in the White Mountain region prior to 1900, the relatively low number of scattered collection sites visited during the subsequent 89 years (1901–1990), and the comparatively even distribution of recent collections.

In the Appendix we have documented forty-three species and two subspecies of *Sphagnum* in New Hampshire. Fifteen species and one subspecies are new state records. These taxa are: *S. andersonianum*, *S. bartlettianum*, *S. brevifolium*, *S. centrale*, *S. compactum*, *S. fallax*, *S. flavicomans*, *S. flexuosum*, *S. henryense*, *S. majus* subsp. *norvegicum*, *S. platyphyllum*, *S. rubellum*, *S. subfulvum*, *S. subtile*, *S. torreyanum*, and *S. viride*.

Species diversity is relatively evenly distributed throughout the counties, with the mountainous Coös, Carroll, and Grafton Counties being the most diverse and Cheshire County the least. Eight species are documented in all counties. The fourteen species reported from nine or more counties likely represent the most common species of *Sphagnum* occurring in the state. Five species are apparently rare in New Hampshire, based on infrequent collection of these species both within New Hampshire and in the nearby

states of New York and Vermont (Andrus 1980; Andrus et al. 1994; McQueen 1992). Two of these species, *S. andersonianum* and *S. brevifolium*, are fairly recent segregates and their apparent rarity may be partly due to earlier collectors overlooking them. Three of the five rare species are restricted to acidic subalpine bogs and fens of the White Mountain subsection.

Collection intensity and diversity within ecoregions indicate that the White Mountain region exhibits the highest diversity with 39 species present (Figure 3; Table 1). In contrast, the North Connecticut River Valley exhibited extremely low *Sphagnum* diversity (7 species), accompanied by few collections, low proportion of surveyed wetland community types, and low total area (Table 1). The Vermont Piedmont, Gulf of Maine Coastal Lowland, and Connecticut Lakes subsections also have relatively low *Sphagnum* species richness (18–20 species) and collection intensity. Of these, only the Connecticut Lakes subsection had *Sphagnum* collections from more than 50% of the wetland community types.

DISCUSSION

Since the Andrews (1906) list of New England Sphagnaceae, there have been many changes in species concepts in this family. For instance, *Sphagnum cymbifolium* Ehrh. (Andrews 1906) likely encompasses specimens of *S. centrale*, *S. henryense*, and *S. palustre*. Although many species in Andrews' (1906) list can be traced to synonymies under the current nomenclature, *S. subnitens* Russow & Warnst. and *S. tenerum* (Austin) Warnst. cannot, and therefore were excluded from our tally of species reported by Andrews from New Hampshire. *Sphagnum subnitens*, as it is understood today, does not occur in eastern North America. Andrews' and Warnstorf's concepts of *S. subnitens* included *Sphagnum* species as varied as *S. angermanicum*, *S. flavicomans*, and *S. subfulvum* (Crum 1984; Andrus pers. obs.). *Sphagnum tenerum* (Austin) Warnst. was misapplied to include not only the current *S. tenerum* Sull. & Lesq., but also forms of *S. capillifolium* and *S. russowii*. We have not seen any specimens of *S. tenerum* from New Hampshire, even though it was reported (by prior taxonomic concepts) on Andrews' (1906) list.

Our *Sphagnum* species concept is narrower than those presented by Crum (1984, 1997), especially within the sections *Acu-*

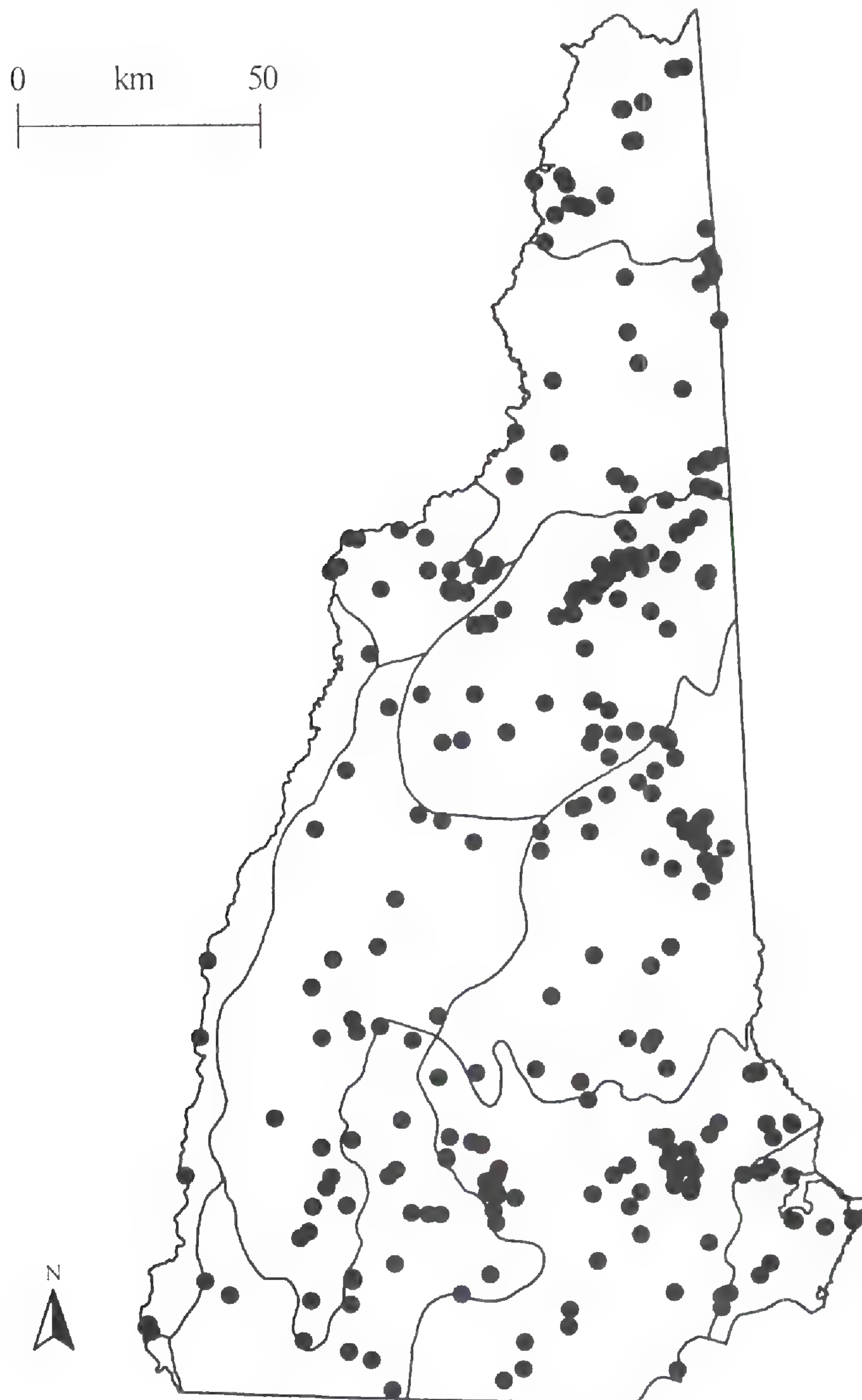


Figure 3. Map of New Hampshire with biophysical subsection outlines showing all known surveyed sites in the state.

tifolia and *Cuspidata*. Employing Crum's (1984, 1997) broader species concept would result in recognition of 34 species and 4 varieties of *Sphagnum* in the state. There are many reasons for being cautious about species delimitation in this genus. For in-

Table 1. Summary of subsection area, wetland diversity, collection intensity, and *Sphagnum* diversity in New Hampshire.

Subsection	Area (km ²)	Wetland Types (primary)	Wetland Types Surveyed	<i>Sphagnum</i> Species Documented	Unicate Species Records
Connecticut Lakes	1500	17 (17)	11	19	38
Mahoosuc–Rangeley Lakes	2502	23 (21)	15	31	145
Vermont Piedmont	771	19 (17)	7	18	36
White Mountains	3211	22 (19)	17	39 (1)	269
Northern Connecticut River Valley	1049	19 (13)	3	7	7
Sunapee Uplands	4206	20 (16)	14	29	99
Sebago–Ossipee Hills and Plain	3630	28 (18)	21	34 (1)	323
Hillsborough Inland Hills and Plains	2463	20 (15)	12	26	112
Gulf of Maine Coastal Plain	3678	27 (20)	18	32	351
Gulf of Maine Coastal Lowland	762	24 (18)	10	20	40

stance, Sæstad (1999) found that the genetic and phenotypic variability in *S. fallax* and *S. isoviitae* overlapped, and thus did not support a distinction between these two species. In addition to phenotypic plasticity within a species, hybridization has also been reported within section *Acutifolia* (Cronberg 1994). Although we are aware of the problems associated with a narrow species concept, we feel that it is the most appropriate way to report the full diversity of *Sphagnum* species in the state at this time. Continued studies utilizing molecular characters and phenotypic plasticity experiments may lead to the clarification and refinement of *Sphagnum* species circumscription.

New Hampshire ranks sixth highest of the 50 states in *Sphagnum* diversity, even though it is only 44th in size (24,097 km²). Of the six smaller states, only New Jersey has more species of *Sphagnum* with 46 species currently reported (Andrus et al. 1994). Many New Hampshire sphagna have boreal centers of distribution, while others such as *S. palustre*, *S. henryense*, *S. recurvum*, and *S. bartlettianum* have more southerly distributions.

We attribute New Hampshire's high diversity of *Sphagnum* to the state's high diversity of wetland communities. These communities reflect a broad range of climatic, geologic, and environmental characteristics at the boreal–temperate–coastal interface. By way of comparison, Minnesota, another state at the boreal–temperate transition, has 40 times the wetland area of New Hampshire, but only 30 *Sphagnum* species (Andrus, unpubl. data), probably because it lacks the elevation range and coastal proximity of New Hampshire. Specifically, the presence of calcareous substrates, subalpine peatlands, and a moderately well developed coastal plain contributes significantly to *Sphagnum* diversity within the state compared to other states.

Mosses are often undercollected in comparison to vascular plants, and this has certainly been the case in New Hampshire. In addition, collection of *Sphagnum* by non-experts usually results in large numbers of collections of a limited number of common species (e.g., *S. girgensohnii*), while neglecting the less common though perhaps equally widespread species (e.g., *S. compactum*). Therefore, without additional careful collecting by knowledgeable bryologists, many widespread, but less common species will appear to be more rare than they actually are. For example, Andrus et al. (1992) indicated a number of sphagna as being rare in Alaska based upon herbarium data, but several sub-

sequent collecting trips to the state revealed that nearly all of these apparent rarities were the result of undercollection.

Although it is likely that additional county records will accrue, it seems unlikely that many new state records will be added to this list, since collection efforts have been well distributed within the state. Although collection intensity is not entirely even (Table 1), collection sites include all wetland types and biophysical subsections present in the state (Figure 3). Based on known *Sphagnum* distributions, the most likely species to be found in future searches of the state include *S. annulatum* H. Lindb. ex Warnst. and *S. tenellum* (Brid.) Bory. Several coastal species of *Sphagnum* that occur in the bordering states of Maine and Massachusetts also may yet be found in New Hampshire's coastal region. These include *S. austinii* Sull. in Austin, *S. molle* Sull., *S. tenerum*, and *S. macrophyllum* Brid.

Natural areas preservation efforts in New Hampshire should integrate information on bryophytes. The distribution of rare peat mosses can be used directly to identify priority wetlands worthy of preservation. In addition, *Sphagnum* and other bryophytes are sensitive indicators of wetland conditions and should be used in the definition and description of community types. This, in turn, will increase the likelihood that representative community types selected for protection will include the full diversity of *Sphagnum* species present in the state and the range of conditions they require for persistence.

The most threatened wetland types in New Hampshire with respect to *Sphagnum* species are rich (calcareous) fens, coastal wetlands, and subalpine wetlands. *Sphagna* restricted to these wetland types include the rich fen species *S. contortum* and *S. warnstorffii*, the coastal species *S. flavicomans* and *S. torreyanum*, and the subarctic-boreal species *S. lindbergii*. Rich fen species are largely restricted to northern New Hampshire and to calcareous glacial deposits within the Connecticut River watershed. New Hampshire calcareous fens are relatively small (< 1 to 5 ha), and many are former pastures (Sperduto and Gilman 1995). Loss of fens through flooding by beavers and humans, succession to more woody composition, and development are conservation concerns. Almost all of New Hampshire's rich fens are privately owned. New Hampshire's coastal wetlands are threatened by continuing development and accompanying drainage. Subalpine sites need to be guarded against degradation by hikers.

Future survey efforts should focus on several current priorities: 1) verification of historical records, especially for *Sphagnum brevifolium*, to clarify whether or not these species are extant in the state; 2) collection efforts in undercollected geographic areas; and 3) specific surveys for rare peat mosses and surveys in rare community types.

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APPENDIX

CHECKLIST OF *SPHAGNUM* IN NEW HAMPSHIRE

Collection numbers are provided when available, otherwise a comma and a year follow the collector. We have included all numbers from Eaton and Faxon S.B.A. and Faxon N.A.S. that were examined, since these specimens were widely distributed and are widely available for reference. However, more recent collections precede each of the exsiccatae in the list because the exsiccatae specimens were collected over 100 years ago and the species may no longer occur in these historical locations. Species that are known from only two or fewer collection sites are marked with an asterisk.

Habitat comments include general nutrient status, microtopographic position, and peatland types where the species are found in New Hampshire. Habitat comments are informed in part by relationships of *Sphagnum* species to plant communities and pH levels described by Sperduto et al. (2000). Nutrient level terminology corresponds to the following pH ranges: oligotrophic (pH 3.5–4.5), weakly minerotrophic (pH 4–5), moderately minerotrophic (pH 4.5–6), minerotrophic (pH 6–7.3), and strongly minerotrophic (pH 7.3+). Microtopographic terms relate to relative height above the water table. Along the gradient from below the water table and increasing in height from the water table, the terms are: pool, carpet, lawn, hummock side, and hummock top (Vitt 1994).

Sphagnum affine Ren. & Cardot – Weakly to moderately minerotrophic. Carpets and low hummocks in sedge fens, tall shrub fens and thickets, and various swamps including black ash seepage swamps. Belknap *Sperduto* 5583c (BH); Carroll *Sperduto* 5502 (BH); Cheshire *Nichols* 194 (BH); Coös *Eaton & Faxon S.B.A.* 153 (BH); Grafton *Cleavitt* 543 (BH), *Faxon N.A.S.* 25, 28 (BH); Hillsborough *Cleavitt* 939 (BH); Merrimack *Cleavitt* 1012 (BH); Rockingham *Cleavitt* 966 (BH); Strafford *Cleavitt* 965 (BH); Sullivan *Andrus* 7669 (BING).

**S. andersonianum* Andrus – Weakly minerotrophic. Low hummocks and hummock sides in very poor ericaceous fens. Grafton *Cleavitt* 1519 (BH).

**S. angermanicum* Melin – Weakly minerotrophic. Forms small patches and loose carpets, often intermixed with other *Sphagnum* species in montane and lowland sedge, shrub-graminoid, and dwarf-medium shrub poor fens. Carroll *Andrus* 9216 (BING); Grafton *Cleavitt* 1517 (BH), *Holcombe* 10 (BH).

S. angustifolium (C. Jens. ex Russow) C. Jens. in Tolf – Oligotrophic to moderately minerotrophic. Carpets and hummock sides, extending far-

- ther up hummocks in mixture with hummock-forming *Sphagnum* species, in open carpets, sedge, shrub-graminoid, and dwarf-medium heath shrub fens and bogs. Belknap *Sperduto* 4974 (BH); Carroll *Cleavitt* 1023 (BH); Cheshire *Nichols* 355 (BH); Coös *Cleavitt* 1527 (BH); Grafton *Cleavitt* 735 (BH), *Eaton & Faxon S.B.A.* 110, 111 (BH); Hillsborough *Cleavitt* 611 (BH); Merrimack *Nichols* 128 (BH); Rockingham Town NH80 (BING); Strafford *Cleavitt* 956 (BH).
- S. bartlettianum* Warnst. – Oligotrophic to weakly minerotrophic. Carpets and low hummocks in dwarf heath shrub bogs and poor fens. Carroll *Sperduto* 5977a (BH); Cheshire *Nichols* 191 (BH); Coös *Sperduto* 5900 (BH); Grafton *Sperduto* 5724 (BH); Hillsborough *Cleavitt* 613 (BH); Rockingham *Andrus* 9058 (BING); Strafford *Nichols* 060 (BH).
- **S. brevifolium* (Lindb. ex Braithw.) C. Jens. – Weakly minerotrophic. Carpets mixed with other *Sphagnum* species in poor fens. Coös *Eaton & Faxon S.B.A.* 82 in part (BH).
- S. capillifolium* (Ehrh.) Hedw. – Oligotrophic to minerotrophic. Dense carpets to tall hummocks in shrub fens and bogs, including exposed alpine and subalpine bogs. Belknap *Sperduto* 5600 (BH); Carroll *Cleavitt* 1160 (BH); Cheshire *Cleavitt* 957 (BH); Coös *Cleavitt* 1529 (BH), *Eaton & Faxon S.B.A.* 41, 42, 47 (BH); Grafton *Cleavitt* 736 (BH); Hillsborough *Cleavitt* 971 (BH); Merrimack *Cleavitt* 614 (BH); Rockingham *Cleavitt* 967 (BH); Strafford *Cleavitt* 962 (BH); Sullivan *Nichols* 332 (BH).
- S. centrale* C. Jens. in Arnell & C. Jens. – Minerotrophic. Pure carpets and low hummocks in sedge and conifer fens. Carroll *Cleavitt* 1161 (BH), *Faxon N.A.S.* 47 (BH); Coös *Cleavitt* 1030 (BH); Grafton *Cleavitt* 1031 (BH); Hillsborough *Sperduto* 5584 (BH); Merrimack *Cleavitt* 615 (BH); Rockingham *Andrus* 9050 (BING); Strafford *Hodgdon*, 1956 (NHA); Sullivan *Andrus* 7686 (BING).
- S. compactum* DC. in Lam. & DC. – Oligotrophic. In New Hampshire the species is mainly a pioneer and can form dense carpets in seepy places over exposed bedrock, sand, or bare peat. Coös *Pease & Andrews*, 1918 (YU); Grafton *Cleavitt* 1175, 1522 (BH); Strafford *Sperduto* 5839 (BH).
- S. contortum* Schultz – Moderately to strongly minerotrophic. Loose carpets in constantly moist microsites within calcareous fens and flarks. Belknap *Sperduto* 4995b (BH); Coös *Cleavitt* 1431 (BH); Grafton *Cleavitt* 1032 (BH), *Eaton & Faxon S.B.A.* 138, 139 (BH); Rockingham *Nichols* 049 (BH); Sullivan *Andrus* 7683 (BING).
- S. cuspidatum* Ehrh. ex Hoffm. – Oligotrophic to weakly minerotrophic. Often with *S. majus* in pools or carpets in open microsites of bogs and poor fens with sparse to dwarf shrub cover. Belknap *Sperduto* 5583a (BH); Carroll *Sperduto* 5012 (BH); Cheshire *Nichols* 198 (BH); Coös *Sperduto* 5753 (BH); Grafton *Cleavitt* 529 (BH); Hillsborough *Cleavitt* 616 (BH); Merrimack *Cleavitt* 617 (BH); Rockingham Town NH67 (BING); Strafford *Hodgdon & Barrett* 15,505 (NHA); Sullivan *Nichols* 324 (BH).
- S. fallax* (Klinggr.) Klinggr. – Oligotrophic to weakly minerotrophic. Often extensive pure carpets and hummock bases in a wide variety of poor fen and bog habitats; absent from alpine bogs. Belknap *Sperduto* 4973 (BH); Carroll *Cleavitt* 1019 (BH); Cheshire *Nichols* 209 (BH); Coös *Cleavitt* 1018 (BH); Grafton *Cleavitt* 530 (BH); Hillsborough *Cleavitt* 618 (BH);

- Merrimack Town NH8 (BING); Rockingham Andrus 9025 (BING); Strafford Hodgdon, 1956 (NHA); Sullivan Andrus 7679 (BING).
- S. fimbriatum* Wils. in Wils. & Hook. f. – Minerotrophic. Low to medium hummocks in sedge and shrub-graminoid fens, tall shrub fens and thickets, and margins of bogs and poor fens. Belknap *Sperduto* 4995a (BH); Cheshire Nichols 193 (BH); Coös Andrews, 1917 (BH); Grafton Cleavitt 531 (BH); Hillsborough Hodgdon & Roberts 10,025 (NHA); Merrimack Cleavitt 619 (BH); Rockingham Town NH30 (BING); Strafford Cleavitt 963 (BH); Sullivan Andrus 7668 (BING).
- S. flavicomans* (Cardot) Warnst. – Oligotrophic to weakly minerotrophic. Medium to tall hummocks in bogs and poor fens. Belknap *Sperduto* 5603 (BH); Coös Austin, 1872 (NY); Rockingham Town NH85 (BING), *Sperduto* 5195 (BH).
- S. flexuosum* Dozy & Molk. – Oligotrophic to moderately minerotrophic. Carpets in shrub and shrub-graminoid fens and fen margins. Belknap *Sperduto* 5588 (BH); Carroll *Sperduto* 5791 (BH); Cheshire Nichols 354 (BH); Coös Eaton & Faxon S.B.A. 108, 109 (BH); Hillsborough Nichols 271 (BH); Merrimack Cleavitt 620 (BH); Rockingham Andrus 9060 (BING); Sullivan Andrus 7666 (BING).
- S. fuscum* (Schimp.) Klinggr. – Oligotrophic. Medium to tall dense hummocks in a wide range of habitats, although usually in open microsites and most common in alpine bogs and dwarf to tall shrub fens and bogs. Belknap *Sperduto* 5599 (BH); Carroll Cleavitt 1027 (BH); Coös Hodgdon 11,539 (NHA); Grafton Cleavitt 732 (BH), Eaton & Faxon S.B.A. 33, 34 (BH); Hillsborough Andrus 9036 (BING); Merrimack Nichols 151 (BH); Rockingham Town NH78 (BING); Strafford Cleavitt 961 (BH); Sullivan Nichols 333 (BH).
- S. girgensohnii* Russow – Oligotrophic to minerotrophic. Carpet patches in swamps and wet conifer forest, carpets to low hummocks in alpine bogs, and along the margins of poor sedge fens. Carroll Cleavitt 1024 (BH); Cheshire Bechtel 033 (BH); Coös Cleavitt 1236 (BH), Eaton & Faxon S.B.A. 1, 5, 7, 9, 10 (BH), Faxon N.A.S. 24 (BH); Grafton Cleavitt 532 (BH), Eaton & Faxon S.B.A. 4, 8 (BH), Faxon N.A.S. 23 (BH); Hillsborough Nichols 019 (BH); Merrimack Cleavitt 622 (BH); Rockingham Cleavitt 968 (BH); Strafford Hodgdon 12,252 (NHA); Sullivan Andrus 7676 (BING).
- S. henryense* Warnst. – Weakly to moderately minerotrophic. Low to medium hummocks in a variety of shrub, sedge, and shrub-graminoid poor to intermediate fen and swamp habitats. Belknap Cleavitt 1512 (BH); Carroll Andrus 9255 (BING); Cheshire Cleavitt 928 (BH); Coös Bartlett 1210 (BH); Grafton Cleavitt 1524 (BH); Hillsborough Cleavitt 940 (BH); Merrimack Cleavitt 623 (BH); Rockingham Cleavitt 624 (BH); Strafford Hodgdon 12,251 (NHA); Sullivan Andrus 7670 (BING).
- S. inundatum* Russow – Weakly minerotrophic. Thick carpets in poor to intermediate fens. Belknap *Sperduto* 5595 (BH); Carroll Andrus 9230 (BING); Grafton *Sperduto* 4253 (BH); Hillsborough Cleavitt 937 (BH); Rockingham Town NH53 (BING); Sullivan Andrus 7682 (BING).
- S. isoviitae* Flatberg – Oligotrophic to weakly minerotrophic. Carpets in a wide range of open microsites in poor to intermediate fens. Belknap

- Sperduto* 5471 (BH); Carroll *Sperduto* 5027 (BH); Coös *Sperduto* 5757 (BH); Grafton *Sperduto* 4923 (BH), Hillsborough *Nichols* 372 (BH); Merrimack *Cleavitt* 625 (BH); Rockingham *Andrus* 9025 (BING); Strafford *Nichols* 061 (BH); Sullivan *Nichols* 329 (BH).
- S. lescurii* Sull. in Gray – Weakly to moderately minerotrophic. Ruderal species found in a wide range of habitats, particularly habitats with fluctuating water levels, mostly in sprawling patches in rock seeps and lake and streamside sedge or shrub-graminoid fens. Belknap *Carter*, 1902 (BH); Carroll *Cleavitt* 1169 (BH); Cheshire *Nichols* 197 (BH); Coös *Sperduto* 5185 (BH); Grafton *Cleavitt* 1405 (BH), *Eaton & Faxon S.B.A.* 145, 146 (BH); Hillsborough *Cleavitt* 938 (BH); Merrimack *Cleavitt* 627 (BH); Rockingham *Town NH*57 (BING); Sullivan *Andrus* 7682 (BING).
- **S. lindbergii* Schimp. in Lindb. – Weakly minerotrophic. Carpets in high elevation heath balds and alpine bogs. Coös *Cleavitt* 1220 (BH), *Eaton & Faxon S.B.A.* 82, 83 (BH).
- S. magellanicum* Brid. – Oligotrophic to weakly minerotrophic. Carpets and hummocks in a wide variety of peatlands, especially common in open dwarf to tall shrub fens and bogs and conifer fens. Belknap *Sperduto* 5601 (BH); Carroll *Cleavitt* 1022 (BH); Cheshire *Nichols* 196 (BH); Coös *Cleavitt* 1530 (BH), *Faxon N.A.S.* 28, 33 (BH); Grafton *Cleavitt* 1359 (BH), *Faxon N.A.S.* 29, 35 (BH); Hillsborough *Cleavitt* 628 (BH); Merrimack *Nichols* 109 (BH); Rockingham *Town NH*58 (BING); Strafford *Hodgdon & Barrett* 15,503 (NHA); Sullivan *Fujiyama*, 1918 (BH).
- S. majus* (Russow) C. Jens. subsp. *majus* – Oligotrophic. Pools and lawns in very poor fens and bogs. Carroll *Sperduto* 5499 (BH); Grafton *Eaton & Faxon S.B.A.* 101 (BH); Hillsborough *Sperduto* 4901 (BH); Rockingham *Sperduto* 4915 (BH); Strafford *Sperduto* 5702a (BH).
- S. majus* subsp. *norvegicum* Flatberg – Weakly minerotrophic. Lawns in poor sedge fens and pond margins. Carroll *Andrus* 9214 (BING); Coös *Eaton and Faxon S.B.A.* 100 (BH); Grafton *Cleavitt* 1511 (BH).
- S. palustre* L. – Weakly to moderately minerotrophic. Carpets and hummocks in fens and swamps. Belknap *Sperduto* 5481 (BH); Carroll *Cleavitt* 1156 (BH); Cheshire *Bechtel* 034 (BH); Coös *Sperduto* 4871 (BH); Grafton *Sperduto* 4924a (BH); Hillsborough *Andrus* 9035 (BING); Merrimack *Allen* 10,046 (MO); Rockingham *Cleavitt* 629 (BH); Strafford *Cleavitt* 964 (BH); Sullivan *Nichols* 334 (BH).
- S. papillosum* Lindb. – Weakly minerotrophic. Thick carpets and low hummocks in open microsites in dwarf to medium heath shrub fens. Belknap *Sperduto* 5587 (BH); Carroll *Sperduto* 5856a (BH); Cheshire *Nichols* 228 (BH); Coös *Cleavitt* 1407 (BH); Grafton *Cleavitt* 734 (BH), *Eaton & Faxon S.B.A.* 163 (BH); Hillsborough *Cleavitt* 597 (BH); Merrimack *Nichols* 378 (BH); Rockingham *Town NH*28 (BING); Strafford *Cleavitt* 914 (BH).
- S. platyphyllum* (Lindb. ex Braithw.) Sull. ex Warnst. – Weakly to moderately minerotrophic. Often found in sprawling patches alongside *S. lescurii* on shores of ponds and lakes, along streams, and margins of sedge or shrub-graminoid fens. Carroll *Andrus* 9229 (BING); Hillsborough *Cleavitt* 937 (BH); Rockingham *Nichols* 033 (BH), *Town NH*25 (BING).
- S. pulchrum* (Lindb. ex Braithw.) Warnst. – Oligotrophic to weakly minerotrophic. Often forming floating mats but also in lawns or carpets in poor

- fens among sedges and usually with sparse or dwarf shrub cover. Belknap *Sperduto* 5474b (BH); Carroll *Cleavitt* 1157 (BH); Coös *Faxon N.A.S.* 49 (BH); Grafton *Sperduto* 5726 (BH); Hillsborough *Nichols* 278 (BH).
- S. pylaesii* Brid. – Oligotrophic to weakly minerotrophic. Growing in prostrate to somewhat erect mats over rock or submerged in fen pools. Carroll *Farlow Reliquiae Farlowianae* 547 (BH); Grafton *Cleavitt* 1518 (BH), *Faxon N.A.S.* 35, 39 (BH); Strafford *Sperduto* 4909b (BH).
- S. quinquefarium* (Lindb. ex Braithw.) Warnst. – Weakly minerotrophic. Carpets in conifer fens and over rock or mineral soil at higher elevations. Coös *Andrews, 1917* (BH), *Sperduto* 5510 (BH); Grafton *Cleavitt* 652 (BH), *Eaton & Faxon S.B.A.* 36, 37, 39 (BH), *Faxon N.A.S.* 39, 43 (BH).
- S. recurvum* P. Beauv. – Weakly minerotrophic. Carpets in various poor fen habitats, typically at margins of peatlands including lagg and pond border situations. Belknap *Sperduto* 5493 (BH); Carroll *Cleavitt* 1028 (BH); Cheshire *Cleavitt* 919 (BH); Coös *Cleavitt* 1270 (BH); Hillsborough *Cleavitt* 631 (BH); Merrimack *Sperduto* 6079 (BH); Rockingham *Cleavitt* 630 (BH); Strafford *Nichols* 103 (BH).
- S. riparium* Ångstr. – Weakly minerotrophic. Lawns at the margins of bogs and poor fens. Belknap *Sperduto* 5220 (BH); Carroll *Sperduto* 5016 (BH); Coös *Cleavitt* 1520 (BH), *Eaton & Faxon S.B.A.* 86, 87 (BH), *Faxon N.A.S.* 45, 46 (BH).
- S. rubellum* Wils. – Oligotrophic to weakly minerotrophic. Dense carpets (often floating) to low hummocks in open dwarf to medium heath shrub bogs and poor fens. Belknap *Sperduto* 5605 (BH); Carroll *Cleavitt* 1171 (BH); Cheshire *Nichols* 195 (BH); Coös *Sperduto* 4880 (BH); Grafton *Cleavitt* 586 (BH); Hillsborough *Cleavitt* 632 (BH); Merrimack *Town NH5* (BING); Strafford *Sperduto* 4906 (BH); Sullivan *Nichols* 321 (BH).
- S. russowii* Warnst. – Oligotropic to minerotrophic. Carpets and hummock sides, often mixed with other species in poor shrub fens, alpine and subalpine bogs, and wet sites in conifer forests. Belknap *Sperduto* 5583b (BH); Carroll *Cleavitt* 1021 (BH); Coös *Cleavitt* 1020 (BH), *Faxon N.A.S.* 55, 56 (BH); Grafton *Cleavitt* 581 (BH), *Eaton & Faxon S.B.A.* 19 (BH); Hillsborough *Cleavitt* 971 (BH); Merrimack *Quillinan* 94-101-35 (BH); Rockingham *Cleavitt* 633 (BH); Strafford *Sperduto* 5710 (BH).
- S. squarrosum* Crome – Moderately minerotrophic. Carpets in conifer fens, at margins of poor fens, and in seepage swamps, forest seeps and other shady, moist situations. Carroll *Sperduto* 5015 (BH); Coös *Engstrom, 1996* (BH), *Eaton & Faxon S.B.A.* 67, 69, 70, 71 (BH); Grafton *Cleavitt* 1406 (BH), *Faxon N.A.S.* 53, 59, 60 (BH); Hillsborough *Cleavitt* 969 (BH); Merrimack *Cleavitt* 634 (BH); Rockingham *Sperduto* 5342 (BH); Strafford *Hodgdon* 14,594 (NHA); Sullivan *Andrus* 7680 (BING).
- **S. subfulvum* Sjørs – Strongly minerotrophic. Hummocks in open sites in intermediate to rich fens. Sullivan *Andrus* 7667, 7671 (BING).
- S. subsecundum* Nees in Sturm – Minerotrophic. Carpets to low hummocks along open margins of poor fens. Belknap *Sperduto* 5590 (BH); Carroll *Sperduto* 5494a (BH), *Faxon N.A.S.* 67 (BH); Coös *Eaton & Faxon S.B.A.* 128, 135 (BH); Grafton *Eaton & Faxon S.B.A.* 133, 136 (BH); Sullivan *Andrus* 7685 (BING).
- S. subtile* (Russow) Warnst. – Oligotrophic to weakly minerotrophic. In low

- hummocks in shaded microsites of poor conifer fens and bogs, including montane sloping fens. Carroll *Andrus* 9243 (BING); Coös *Sperduto* 4877 (BH); Grafton *Cleavitt* 1528 (BH); Merrimack *Nichols* 131 (BH); Rockingham *Town NH*16 (BING); Sullivan *Andrus* 7677 (BING).
- S. teres* (Schimp.) Ångstr. in Hartm. – Moderately to strongly minerotrophic. Carpets to hummocks in intermediate to rich fens and seepage forest. Carroll *Andrus* 9267 (BING); Coös *Cleavitt* 1029 (BH); Grafton *Cleavitt* 737 (BH); Sullivan *Andrus* 7680 (BING).
- S. torreyanum* Sull. – Weakly minerotropic. Pools or lawns in poor fens with sparse and dwarf shrub cover or submerged along lake margins. Belknap *Sperduto* 5604 (BH); Carroll *Cleavitt* 1344 (BH); Cheshire *Nichols* 230 (BH); Coös *Sperduto* 5896 (BH); Hillsborough *Sperduto* 5610 (BH), *Cher-rington*, 1904 (BH); Merrimack *Town NH*2 (BING); Rockingham *Cleavitt* 635 (BH); Sullivan *Nichols* 330 (BH).
- S. viride* Flatberg – Weakly minerotrophic. Pools and lawns in poor fens. Carroll *Cleavitt* 1026 (BH); Hillsborough *Andrus* 9031 (BING); Merrimack *Town NH*12 (BING); Rockingham *Andrus* 9029 (BING).
- S. warnstorffii* Russow – Moderately to strongly minerotrophic. Carpets and hummocks in open calcareous sedge fens, seepage swamps, and other minerotrophic fen and swamp situations. Carroll *Sperduto* 5768 (BH); Coös *Sperduto* 4392 (BH); Grafton *Sperduto* 4391 (BH), *Eaton & Faxon S.B.A.* 23, 28 (BH).
- S. wulfianum* Girg. – Minerotrophic. Carpets and loose hummocks in shady microsites of treed fens and moist conifer forests of central and northern New Hampshire. Carroll *Sperduto* 6191 (BH); Coös *Cleavitt* 985 (BH), *Eaton & Faxon S.B.A.* 73 (BH); Grafton *Sperduto* 6192 (BH), *Eaton & Faxon S.B.A.* 74, 75 (BH).

FLORISTIC DIVERSITY IN THE EXPERIMENTAL
WATERSHEDS OF THE HUBBARD BROOK
EXPERIMENTAL FOREST, NEW HAMPSHIRE, USA

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ABSTRACT. Complete abundance-annotated botanical inventories of managed and unmanaged forested areas provide critical baseline data for the long term monitoring of floristic diversity. Such data are essential in identifying species at risk of local or regional extirpation, in tracking rates of exotic invasion, and in the evaluation of species diversity effects arising from natural and anthropogenic disturbance. The reaction of forest herbaceous species to disturbance, and their subsequent recovery rates, have been little studied to date. This study documents the complete floras of seven experimental watersheds of the Hubbard Brook Experimental Forest, compares their relative floristic characters, and provides baseline data for long term diversity monitoring at the Hubbard Brook Experimental Forest. The two watersheds having undergone experimental clearcuts in the recent past were found to differ significantly in elements of the herbaceous understory. These differences were not reflected in tree data and suggest that forest management policies based on tree recovery times may underestimate true floristic recovery periods, and threaten diversity over the long term.

Key Words: flora, floristic diversity, understory succession, herbaceous recovery, forest ecosystems, Long Term Ecological Reserve, Hubbard Brook Experimental Forest

According to classical theory, secondary succession of the understory in disturbed forests is largely a factor of canopy development and competition (Bormann and Likens 1979; Kimmins 1997). Species richness in secondary forests is believed to be closely tied to successional stages. Theoretically, an increase in diversity is expected in the early stages, followed by a decrease as the canopy closes, followed by another gradual rise as the woodland flora is restored (Bormann and Likens 1979; Kimmins 1997). In New England, Bormann and Likens (1979) observed

that heavily cut hardwood forests initially underwent a dramatic increase in shade-intolerant species, followed by a gradual decline in these species as the canopy developed and light regimes changed. Shade-tolerant species (woodland species) that were able to survive both the loss of the forest canopy and the competitive pressures of the weedy invaders were theorized to be free to increase in abundance once the canopy reached sufficient maturity. Additional woodland species would likely immigrate from surrounding areas and the secondary forest flora would thus, at least in theory, approach and potentially even achieve pre-cut levels of diversity over time.

While the effects of disturbance on floristic diversity have often been speculated upon in the scientific literature, particularly of such catastrophic disturbance as mechanized clearcutting, clear answers continue to elude us (Bratton 1976; Carbonneau 1986; Meier et al. 1995; Peterken and Game 1984; Whitney 1991; Whitney and Foster 1988). Unquestionably, the lack of long term data has inhibited our efforts. The preponderance of data from New England forests have traditionally focused on tree species alone, with understory communities examined only in terms of total biomass or total percent cover in prescribed plots. Studies distinguishing individual herbaceous species are rare, and full inventories of research sites are rarer still.

This study employed complete floristic inventories rather than a plot-based approach because total inventories provide the most accurate measure of species richness, and are therefore best suited for long-term diversity monitoring. While valuable for many applications, plot sampling provides only an estimate of the site's true species richness. Such sampling techniques tend to miss rare species altogether and underestimate contagiously distributed (clumped) species. These restrictions limit the value of plot-based approaches in diversity studies of young forests, where contagious distributions are more common (Kimmins 1997; Whitney 1991), and in mature forests, where rare species have often been found to be among the better indicators of old growth systems (Whitney and Foster 1988). Plots also lack the ability to deal with floristic drift, making local extirpations or introductions difficult to document.

The objectives of this study were to conduct complete inventories of the vascular floras of the Hubbard Brook Experimental Forest (HBEF) watersheds, with population abundance estimates,

and to compare relative floristic similarities between them with respect to past experimental management treatments. These constitute the first complete botanical inventories ever conducted at HBEF and will serve as the baseline for long-term monitoring of floristic diversity, as well as aid in future ecological research within the watersheds.

All the experimental watersheds in the HBEF are secondary forests. This paper focuses on a comparison of the floristic diversity within two watersheds having undergone experimental clearing in the past few decades with that of several of the watersheds consisting of more mature secondary forest.

SITE DESCRIPTION

Study area. The Hubbard Brook Experimental Forest is a 3160 ha Biosphere Reserve in the White Mountain National Forest, New Hampshire, dedicated as a Long Term Ecological Reserve (LTER), and operated by the U.S.D.A. Forest Service's Northeastern Forest Experiment Station. Since the Hubbard Brook Ecosystem Study was founded in 1963, ten small, well-defined experimental watersheds have been delineated in the northeastern section of the bowl-shaped Hubbard Brook Valley. Over 1500 publications have been generated by HBEF researchers, most involving these watersheds, yet complete floristic inventories had never been conducted. Seven of the ten experimental watersheds were inventoried for this study (Figure 1), including five adjacent watersheds on the south- to southeastern-facing slope (W1, W3, W4, W5, W6), located in the town of Woodstock, and two adjacent watersheds on the north-facing slope (W7, W8), located in the town of Ellsworth (Table 1).

The upper portions of most of the watersheds were characterized by a Lyman-Tunbridge soils association or a Tunbridge-Lyman-Rock outcrop complex; the middle third was Beckett series; the lower portion was mostly Berkshire, Marlow, or Peru-Marlow soils (Hubbard Brook Experimental Forest 1996). The watersheds share relatively impermeable bedrock and typical New England acidic, coarse, well-drained soils, derived from glacial tills (Siccamo et al. 1970). Soil texture ranged from fine to very rocky sandy loam and average soil depth was 1.5 m, with shallower soils occupying the upper third of most watersheds. Significant decreases in till depths occurred at 732 m in elevation and above

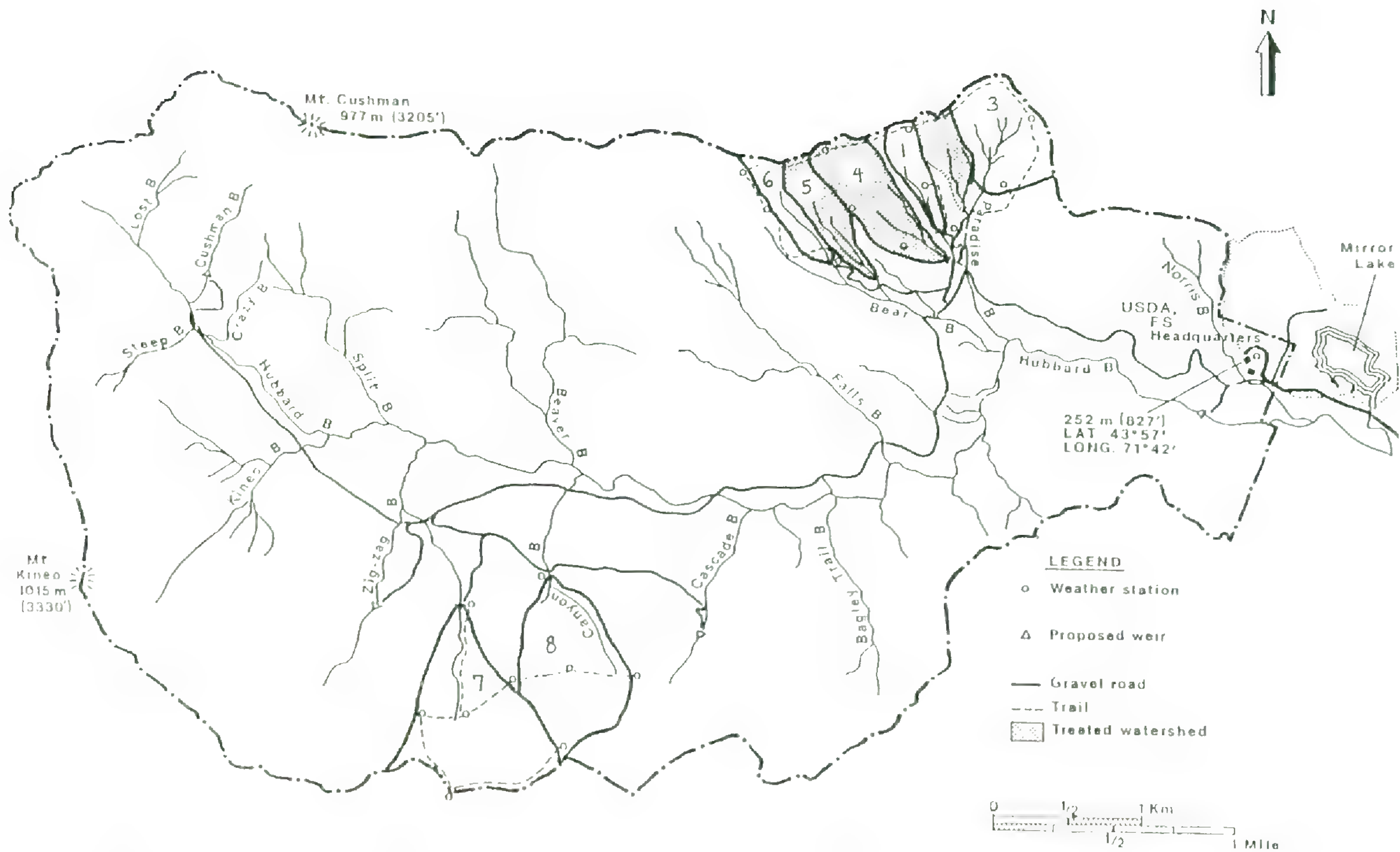


Figure 1. Map of the Hubbard Brook Experimental Forest, showing delineation of the seven experimental watersheds studied. Shading indicates areas that were logged as experimental treatments.

Table 1. Characteristics of the Hubbard Brook experimental watersheds. Percent of total watershed areas attributed as hardwood (HW), mixed hardwood–spruce-fir (CON), and open (OPEN) vegetation class type was determined using the HBEF vegetation map prepared by Cornell University's Resource Information Lab in 1979, and 1987 aerial photography provided by the U.S.D.A. Forest Service, Pemigewasset Station.

WS	Treatment	Slope Aspect	Elevation (m)	Area (ha)	HW %	CON %	OPEN %	Total Species Richness
1	Noncutting treatments	S23W	527–732	11.8	78.0	16.4	5.6	73
3	Reference	S22E	488–747	42.2	84.3	13.6	2.1	75
4	Strip cut 1970–74	S40E	442–747	36.1	93.8	3.0	3.2	89
5	Clearcut 1983–84	S24E	488–762	21.9	87.2	1.0	11.8	114
6	Reference	S32E	549–792	13.2	75.3	22.9	1.8	61
7	Reference	N16W	619–899	76.4	58.6	40.4	1.0	94
8	Reference	N12W	610–905	59.4	34.2	64.8	1.0	71

(Bormann et al. 1970; Federer et al. 1990). At high elevations exposed bedrock was common, but rock outcrops and occasional large boulders occurred at all elevations throughout the Hubbard Brook Valley. The valley was characterized by rather oligotrophic nutrient conditions.

The Hubbard Brook Valley is described by mesic, cool-temperate, humid continental conditions (Whittaker et al. 1974). For more detailed information on the climate of HBEF see Hubbard Brook Ecosystem study site description and research activities (Hubbard Brook Experimental Forest 1996).

Prior to 1895, most of the Hubbard Brook Valley was mature, primary forest (Bormann et al. 1970; Likens and Bormann 1995). The valley was intensively logged between 1895 and 1917 with no evidence of further logging activity or fire after this time. The valley did not experience any serious damage as a result of the 1938 hurricane (C. Cogbill, HBEF researcher, pers. comm.). At the time of this study, the watersheds were characterized by relatively even-aged secondary forests with some older trees present. Two of the watersheds inventoried (W4, W5) were experimentally clearcut within the last thirty years and, hence, were young, even-aged tertiary forests.

Three intergrading vegetation types existed in the experimental watersheds: northern hardwood forest, mixed hardwood–spruce-fir forest, and open areas. Northern hardwood forest typically occupied the lower elevations (440–670 m), and was characterized by the dominant tree species *Fagus grandifolia*, *Acer saccharum*, and *Betula alleghaniensis*, with less abundant populations of *Fraxinus americana*, *A. pensylvanicum*, *A. rubrum*, and *A. spicatum*. Understory vegetation tended to be abundant in these areas and typical shrub species included *Lonicera canadensis*, *Cornus alternifolia*, and *Viburnum alnifolium*. Herbaceous species such as *Dryopteris intermedia*, *Smilacina racemosa*, *Trillium erectum*, *T. undulatum*, *Streptopus roseus*, and *Uvularia sessilifolia* were commonplace on the forest floor. Slopes ranged from 10° to 30°.

Boreal spruce-fir vegetation began to intergrade with the hardwood forest at around 670 m, as well as occurring on mid-to-high elevation rocky outcrops. Trees characterizing the boreal spruce-fir vegetation type include *Abies balsamea*, *Picea rubens*, and *Betula cordifolia*, with less abundant populations of *B. alleghaniensis* and *Sorbus americana*. Understory vegetation was typically less abundant than in pure hardwood areas and could include large areas with virtually no ground flora at all. Shrub species typical of this intergraded forest type included *Viburnum alnifolium*, *Vaccinium myrtilloides*, and *V. angustifolium*. Characteristic herbaceous species included *Dryopteris campyloptera*, *Coptis trifolia*, *Cornus canadensis*, and *Lycopodium obscurum*. These forests were characterized by shallower soils than pure hardwood regions, a decrease in mean temperatures, increased wind stress and precipitation, a reduced growing season (longer periods of snow cover and shorter frost-free periods), and generally more rugged terrain. Slopes of up to 30° were common.

Open areas in the watersheds were primarily represented by the 0.3 ha rain gauge clearings and particularly wide portions of the foot trails, both maintained in the watersheds for the purpose of hydrological research. In a very few cases the floras of small, naturally occurring open areas fell within this vegetation category, although such areas were not common in the HBEF watersheds. An open area was defined as any breach in the canopy of over 10 m², regardless of elevation, estimated by field observer's strides. Tree species in these areas were thus limited primarily to stump shoots (in rain gauge clearings and areas of recently clear-

cut forest) and seedlings of taxa defining either of the two previous vegetation types. Herbaceous species varied widely from site to site, a fact which likely reflected the combined influences of seed bank, surviving woodland species occurrences, and species introductions by human traffic.

Watershed descriptions. Five watersheds were considered “references” for the floristic comparisons in this study; two underwent experimental harvesting treatments in the recent past. Reference watersheds W1, W3, W6, W7, and W8 were last cut in the early 1900s and were hence maturing secondary forests at the time of this study (Table 1). Watershed 1, while designated here as a reference, underwent experimental applications of calcium in the year after its inventory was complete. Watershed 3 encompassed the largest proportion of pure hardwood forest among these references and additionally benefitted from a diverse network of streams and tributaries.

The watershed most frequently used as a vegetation reference by other HBEF researchers (Wayne Martin, HBEF Site Supervisor, pers. comm.) was W6. Its stand composition had been referred to as reasonably representative of climax conditions (Bormann et al. 1970), and its ecological systems had been assessed as mature and in dynamic balance, based upon vegetation biomass and productivity data (Leak 1987; Siccama et al. 1970; Whittaker et al. 1974). An HBEF policy of minimal disturbance of W6 has resulted in the absence of rain gauge clearings, limited foot traffic, and the prohibition of plant collecting within this watershed.

Reference W7 was the largest watershed in the study and had a great variety of observed microhabitats (defined here as specialized areas within the larger habitat, occupied by uniquely different taxa or taxonomic groups). Some examples included several small wetlands not found elsewhere in the study, and numerous small cascades which created stifles and vernal pools throughout both hardwood and mixed coniferous areas. Reference W8 stood somewhat apart from the other watersheds floristically, due to its significantly smaller percent of pure hardwood area (Table 1).

Treatment watersheds W4 and W5 were both young tertiary forests recovering from clearcutting treatments. Watershed 4 was experimentally cut during the winters of 1970 through 1974. A “progressive strip cut” method was used and resulted in the wa-

tershed's total clearance. The watershed was divided into 49 roughly parallel strips, each 25 m wide and oriented east to west along the contours of the slope. In the fall of 1970 every third strip was cut, constituting the first of the series. All merchantable trees were removed from the site and scarification of the soil was encouraged by varying skidder routes across the active strips. In the fall of 1972, the series of strips below the first were cut, and the remaining trees were harvested in the fall of 1974. A more detailed account of this watershed treatment is presented by Martin and Hornbeck (1989).

At the time of this study, W4 was a 26-year-old tertiary forest dominated by dense, relatively even-aged stands of *Prunus pensylvanica*, *Acer pensylvanicum*, *Fagus grandifolia*, and *Betula alleghaniensis*. The canopy was dense and continuous relative to the other watersheds, and consequently, light levels in this watershed may have been lower. While forest undergrowth tended to be sparse, invasive shade-intolerant species persisted from when this watershed was first cleared, and were in evidence wherever the canopy was broken.

Watershed 5 was mechanically whole-tree clearcut over the winter of 1983–84. Once again, all merchantable trees were removed and mechanical scarification of the soil was encouraged. Only limbs and treetops were left on site, resulting in the removal of more than 90% of the aboveground biomass.

At the time of this study, W5 was a 16-year-old tertiary forest dominated by even-aged *Prunus pensylvanica*, *Acer pensylvanicum*, *Fagus grandifolia*, and *Betula alleghaniensis*. Tree regeneration was heavy, making foot travel through this site difficult. The canopy was well developed, however the remains of primary skidder trails were still evident, constituting some of W5's substantial area of open canopy, relative to both reference watersheds and W4. Watershed 5 was also observed to offer a good variety of microhabitats due in part to its topographic heterogeneity. One example of this was a small, well-developed wetland, which was likely iced over during the harvesting operations, and therefore survived relatively intact.

MATERIALS AND METHODS

Reconnaissance field surveys were used to inventory the flora of each watershed according to three vegetation classes: hard-

Table 2. Frequency of occurrence scale suggested by Palmer et al. 1995. A “dominant” species was defined as one constituting approximately 20% or more of all individuals present. “Individuals” of clonal species were defined as ramets.

Rank	Category	Qualitative Description
5	Abundant	Dominant or codominant in one or more common habitats
4	Frequent	Easily seen or found in one or more common habitats, but not dominant
3	Occasional	Widely scattered, but not difficult to find
2	Infrequent	Difficult to find, few individuals or colonies, but found in several locations
1	Rare	Very difficult to find and limited to one or very few locations or uncommon habitats
0	Absent	Not found, but found in a previous survey from the same or similar sites, or was otherwise suspected to occur

wood forest, mixed hardwood–spruce-fir forest, and open areas. Separate inventories were taken for each of these three classes within each of the seven watersheds. The mixed hardwood–spruce-fir forest category represented both areas of pure spruce-fir type vegetation, and the boundary where the spruce-fir and northern hardwood forest types intergraded. This class was identified by a combined presence of 40% or more of *Picea rubens* and *Abies balsamea* in the canopy.

The first weeks of spring (early May) were spent mapping microhabitats and dividing the vegetation classes into segments that could be readily traversed in a field day. These segments were then visited weekly from mid-May through early September. Watersheds 1, 3, 4, 5, and 6 were surveyed during the field seasons of 1995 and 1996; W7 and W8 were surveyed in 1997. Species lists were compiled and voucher specimens were collected, unless doing so would have threatened the existing population. Collections were deposited in the Hodgdon Herbarium (NHA) at the University of New Hampshire, and in numerous cases, duplicates were placed in the Hubbard Brook collection as well.

Estimates of species abundance within each segment were made based upon the rank abundance approach suggested by Palmer et al. (1995; Table 2). This system was used to rank the frequency of occurrence of individuals of a species in relation to the total flora. A “dominant” species was defined as one consti-

tuting roughly 20% or more of the individuals present. In a highly diverse area it was therefore possible to have no species rate in the “abundant” category (5), but rather, several rated only as “frequent” (4). Due to the prevalence of clonal species in this study, “individuals” were defined as ramets. At the end of the field season, data from all segments constituting a watershed’s vegetation class were combined. The proportional area the segment represented was calculated and estimates of species abundance were averaged according to that proportion, yielding an estimate for the entire vegetation class.

Data were analyzed both by vegetation class and total watershed. Total floras were examined compositionally by tree, shrub, and herbaceous communities, and the herbaceous community was further divided into “woodland” and “nonwoodland” species (Teeling 1998). The definition of “woodland species” is adapted from a Peterken and Game (1984) analysis, which partitioned “shade-casters, shade-bearers, and wood-margin species” (p. 159) into a group seen as more representative of undisturbed forests. In this study, we have included forest gap species in the woodland species list. “Nonwoodland” species were thus the shade-intolerant species more associated with open areas or early successional conditions.

Sørensen’s Index of Similarity, expressed as a percentage, was used to compare the watersheds’ total floras. This index measures the number of coinciding species occurrences against the number of theoretically possible co-occurrences (Mueller-Dombois and Ellenberg 1974). The index is described by:

$$ISs = \frac{2c}{a + b} \times 100$$

where *a* is the number of species in area A, *b* is the number of species in area B, and *c* is the number of species in common to both areas A and B.

The seven watersheds, each with three vegetation classes, produced 21 “study units” with species richness and corresponding abundance data (Table 3). Analysis of covariance (ANCOVA) was used to examine relationships between watershed and vegetation class (both classification data), and species richness in these units, while adjusting for any effects of area (continuous data; Ostle and Mensig 1975). Total species richness was the dependent

Table 3. Area and total species richness of the 21 “study units”, representing the hardwood (HW), mixed hardwood–spruce-fir (CON), and open (OPEN) vegetation classes within each of the seven watersheds.

	Study Unit	Area (ha)	Total Species Richness
1	HW1	9.2	55
2	HW3	35.7	63
3	HW4	33.8	69
4	HW5	19.1	90
5	HW6	9.9	53
6	HW7	44.7	74
7	HW8	20.3	60
8	CON1	1.9	54
9	CON3	5.8	47
10	CON4	1.1	41
11	CON5	0.2	60
12	CON6	3.0	30
13	CON7	30.9	65
14	CON8	38.5	44
15	OPEN1	0.66	47
16	OPEN3	0.87	53
17	OPEN4	1.16	54
18	OPEN5	2.60	74
19	OPEN6	0.25	23
20	OPEN7	0.80	65
21	OPEN8	0.60	52

variable, area was the independent covariate, and watershed and vegetation class were the independent noncomitant variables. Four subsets of species richness were also tested to examine possible associations to watershed characteristics. These were tree species, herbaceous species, woodland herbaceous species, and nonwoodland herbaceous species. There was insufficient replication to include interaction terms in these analyses. Protected Tukey’s pairwise comparison tests were used to identify differences between individual watersheds.

As species richness is only a presence-absence indicator, population sizes of tree, herbaceous, woodland, and nonwoodland species within the watersheds were compared via abundance rank distribution patterns. These comparisons were made by hardwood and mixed hardwood–spruce-fir vegetation class and were viewed as a way of comparing the general establishment and vigor of individual species populations in the tree, total herbaceous, and

woodland herbaceous subsets. Open areas were not analyzed. Species were sorted according to abundance ranks into four categories (due to the scarcity of data in abundance ranks 4 and 5, these two ranks were combined). Chi-square test for independence was used to compare abundance distribution patterns of species in each of the watersheds.

RESULTS

One hundred and fifty-five species were encountered in the combined 261 ha of the seven experimental watersheds, only 3.2% of which (or five species) were non-native (Appendix). Eighty-three of those species, or 70.3% of all herbaceous species, were designated as woodland herbaceous species. Clearcut watershed W5 was richest overall, while W6 was least rich (Table 1). In all watersheds and in each of the three vegetation classes, the herbaceous community proved to be far richer than either the tree or shrub communities, with hardwood areas showing the greatest herbaceous diversity overall (Figures 2 and 3).

Analysis of Variance (ANOVA) testing, using watershed area as the independent variable and species richness as the dependent variable, indicated that area was not a significant factor in determining species richness within the watersheds. Sørensen's Index of Similarity showed strong floristic affinities between the reference watersheds, and lesser affinities between the references and treatment watersheds. Treatment watersheds W4 and W5 were about as similar to one another (74.3%) as the references were to each other (mean 76.0%). The total range of floristic similarity (Table 4) was between 85.3% (W1 and W3) and 59.8% (W5 and W6).

While no significant variables were identified in the ANCOVA using tree species alone, all analyses that included herbaceous species data provided significant results (Table 5). In successive ANCOVAs using the total species list, herbaceous species only, and woodland herbaceous species only, both watershed and vegetation class proved to be significantly associated with species richness. Watershed was the only variable significantly associated with nonwoodland herbaceous species richness. Area was not a significant predictor of species richness in any of the datasets used. Results of protected Tukey's pairwise comparison tests most often revealed significant differences in species richness between

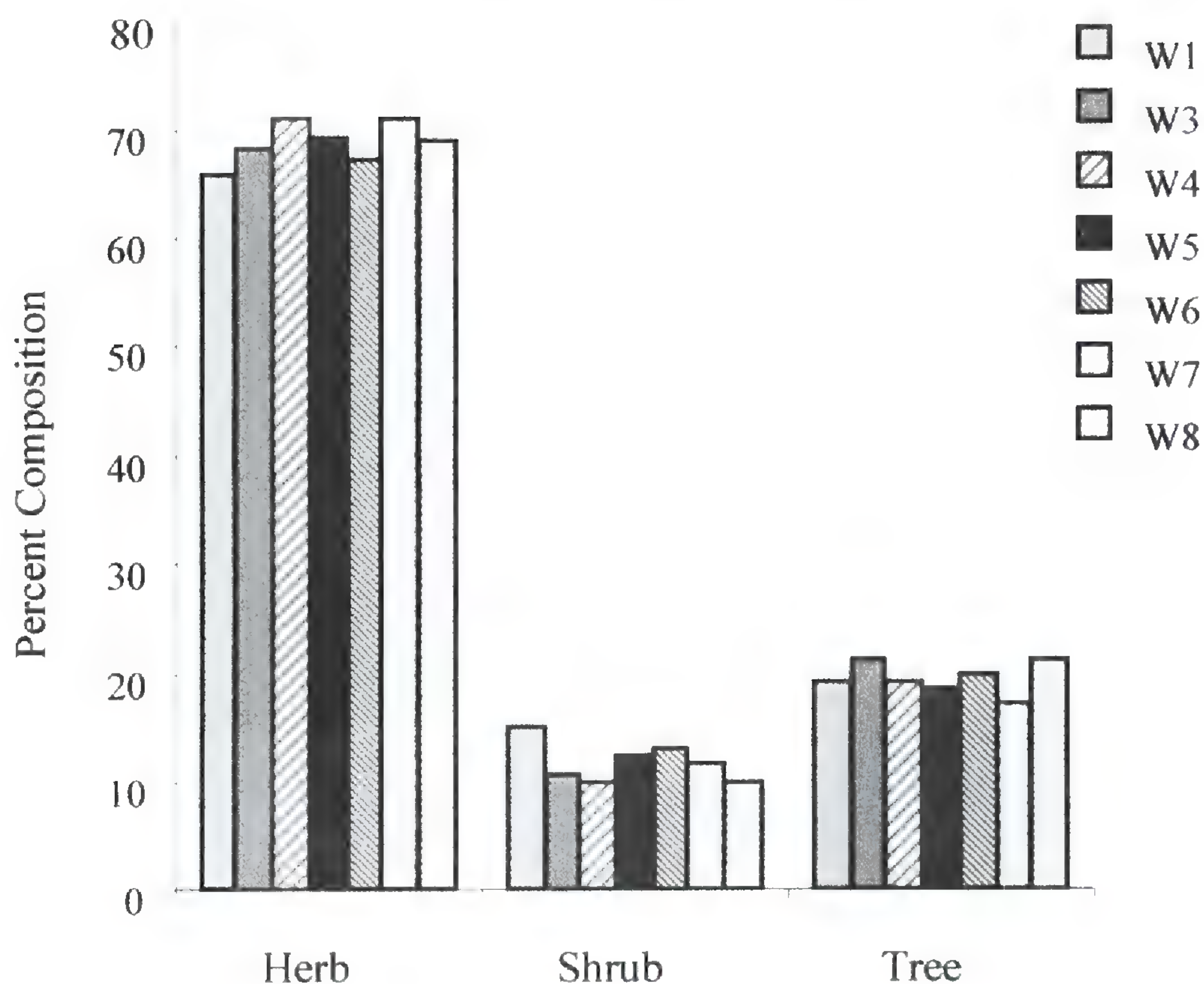


Figure 2. Percent composition of total watershed floras dominated by the herbaceous, shrub, and tree communities.

treatment watersheds W4 and W5, and the two references representing richness extremes: W6 being the least rich, and W7 being the richest (Table 6).

Comparisons of rank abundance distribution patterns of tree species revealed no statistically significant differences in forested regions of the seven watersheds, according to Chi-square tests for independence (Table 7). In contrast, distribution patterns of both herbaceous and woodland herbaceous species in hardwood regions were found to differ significantly across the watersheds (Figures 4 and 5). Removal of W5 data from the herbaceous analysis resulted in the loss of significance, while removal of W4, W5, or W7 all resulted in reversing test results in the woodland herbaceous species analysis.

DISCUSSION

As watershed area was not found to be a significant factor affecting species richness, floristic differences between the seven

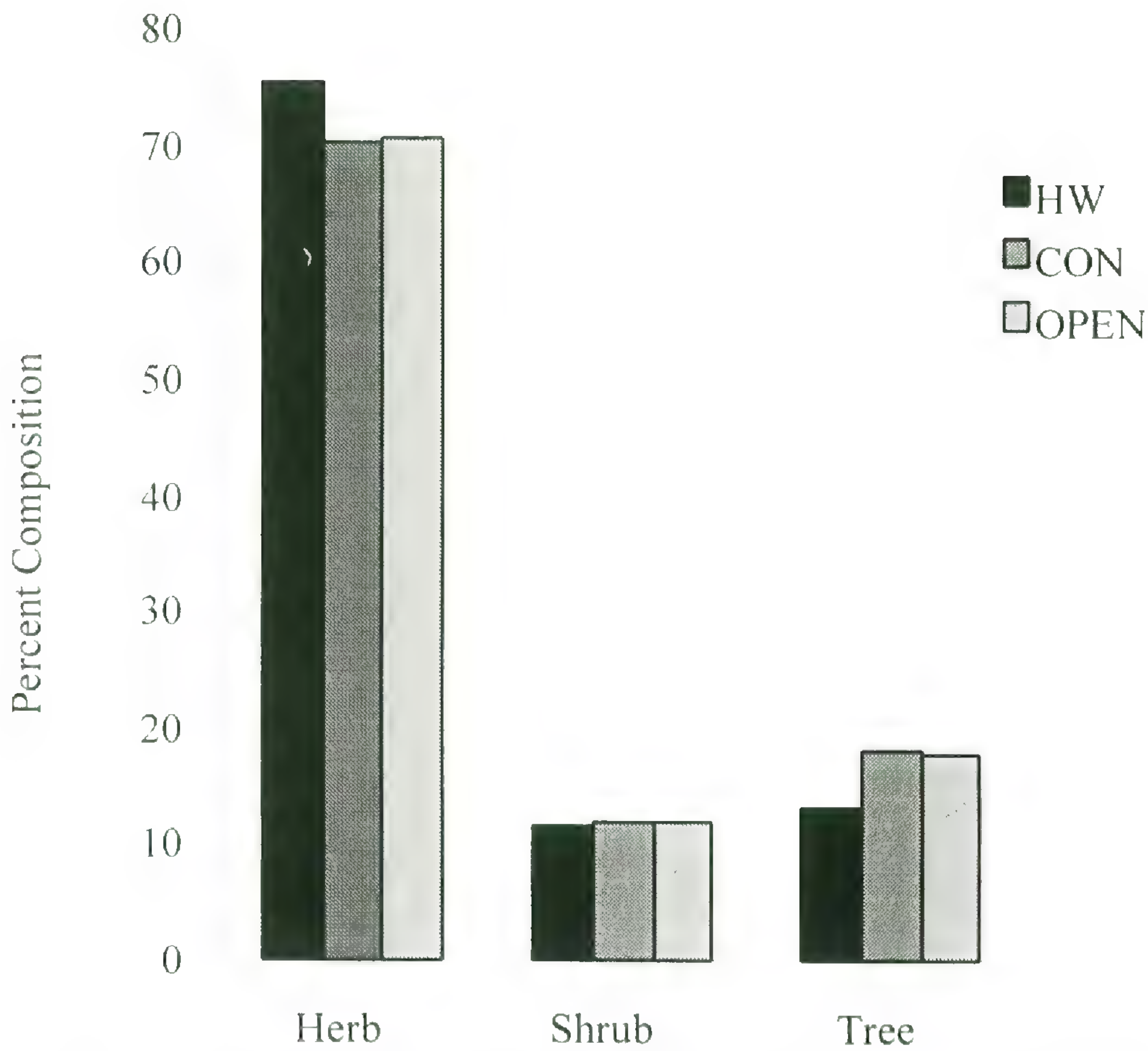


Figure 3. Percent composition of the hardwood (HW), mixed hardwood–spruce-fir (CON), and open (OPEN) vegetation class floras dominated by the herbaceous, shrub, and tree communities.

Table 4. Sørensen’s Index of Similarity matrix for the watersheds studied. Main diagonal (bold) is the number of species in each watershed, above the main diagonal is the number of species in common to both watersheds, and below the main diagonal is Sørensen’s percent floristic similarity. Mean similarity is 73.5%. Standard deviation from the mean is 5.57%.

	W1	W3	W4	W5	W6	W7	W8
W1	68	61	62	62	49	58	52
W3	85.3	75	65	65	52	62	54
W4	79.5	79.8	88	75	54	63	59
W5	68.1	68.8	74.3	114	52	73	60
W6	76.6	77.0	73.0	59.8	61	54	49
W7	72.5	74.3	70.0	70.9	71.1	92	65
W8	74.8	74.0	74.2	64.9	74.8	79.8	71

Table 5. Results of linear ANCOVA models for tree, total, herbaceous, woodland herbaceous, and nonwoodland herbaceous species richness (S), and noncomitant variables area (A), watershed (W), and vegetation class (VC).

	S = A+W+VC+k	S = W+VC+k	S = W+k	S = VC+k
Tree	R ² = 0.411 A (<i>p</i> = 0.477) W (<i>p</i> = 0.496) VC (<i>p</i> = 0.918)			
Total	R ² = 0.899 A (<i>p</i> = 0.953) W (<i>p</i> < 0.001) VC (<i>p</i> = 0.005)	R ² = 0.899 W (<i>p</i> < 0.001) VC (<i>p</i> < 0.001)	R ² = 0.639 W (<i>p</i> = 0.013)	R ² = 0.260 VC (<i>p</i> = 0.066)
Herbaceous	R ² = 0.898 A (<i>p</i> = 0.898) W (<i>p</i> = 0.001) VC (<i>p</i> = 0.003)	R ² = 0.898 W (<i>p</i> < 0.001) VC (<i>p</i> < 0.001)	R ² = 0.581 W (<i>p</i> = 0.033)	R ² = 0.317 VC (<i>p</i> = 0.032)
Woodland	R ² = 0.907 A (<i>p</i> = 0.793) W (<i>p</i> = 0.003) VC (<i>p</i> = 0.001)	R ² = 0.906 W (<i>p</i> < 0.001) VC (<i>p</i> < 0.001)	R ² = 0.478 W (<i>p</i> = 0.114)	R ² = 0.428 VC (<i>p</i> = 0.007)
Nonwoodland	R ² = 0.873 A (<i>p</i> = 0.555) W (<i>p</i> < 0.001) VC (<i>p</i> = 0.038)	R ² = 0.868 W (<i>p</i> < 0.001) VC (<i>p</i> = 0.033)	R ² = 0.768 W (<i>p</i> = 0.001)	R ² = 0.100 VC (<i>p</i> = 0.386)

Table 6. Tukey's pairwise comparison test results for total, herbaceous, woodland herbaceous, and nonwoodland species richness.

	Significant Watershed Comparisons	<i>p</i> Value
Total	W5 and W6	$p < 0.001$
	W6 and W7	$p < 0.001$
Herbaceous	W5 and W6	$p < 0.001$
	W6 and W7	$p < 0.001$
Woodland	W4 and W7	$p < 0.001$
	W6 and W7	$p < 0.001$
Nonwoodland	W1 and W5	$p < 0.001$
	W3 and W5	$p < 0.001$
	W5 and W6	$p = 0.001$
	W5 and W7	$p = 0.001$
	W5 and W8	$p = 0.001$

watersheds were assumed to be dependent on treatment, stand age, aspect, and environmental site conditions. Overall, the seven watersheds showed a generally high degree of floristic similarity. This was expected for largely contiguous parcels within the HBEF. That the similarity between treatment watersheds W4 and W5 was slightly lower than the mean similarity between the five references (which included noncontiguous areas, with both north- and south-facing aspects) probably reflects W4 and W5's different

Table 7. Chi-square test for independence results for abundance rank distributions of tree, total herbaceous, woodland herbaceous, and nonwoodland herbaceous species in the HBEF watersheds. Floras were analyzed by hardwood (HW) and mixed hardwood–spruce-fir (CON) vegetation classes. Critical value was 37.16.

	Vegetation Class	χ^2	Significance
Tree	HW	23.33	No
	CON	10.48	No
Herbaceous	HW	42.49	Yes
	CON	23.90	No
Woodland	HW	40.04	Yes
	CON	28.73	No
Nonwoodland	HW	5.11	No
	CON	4.08	No

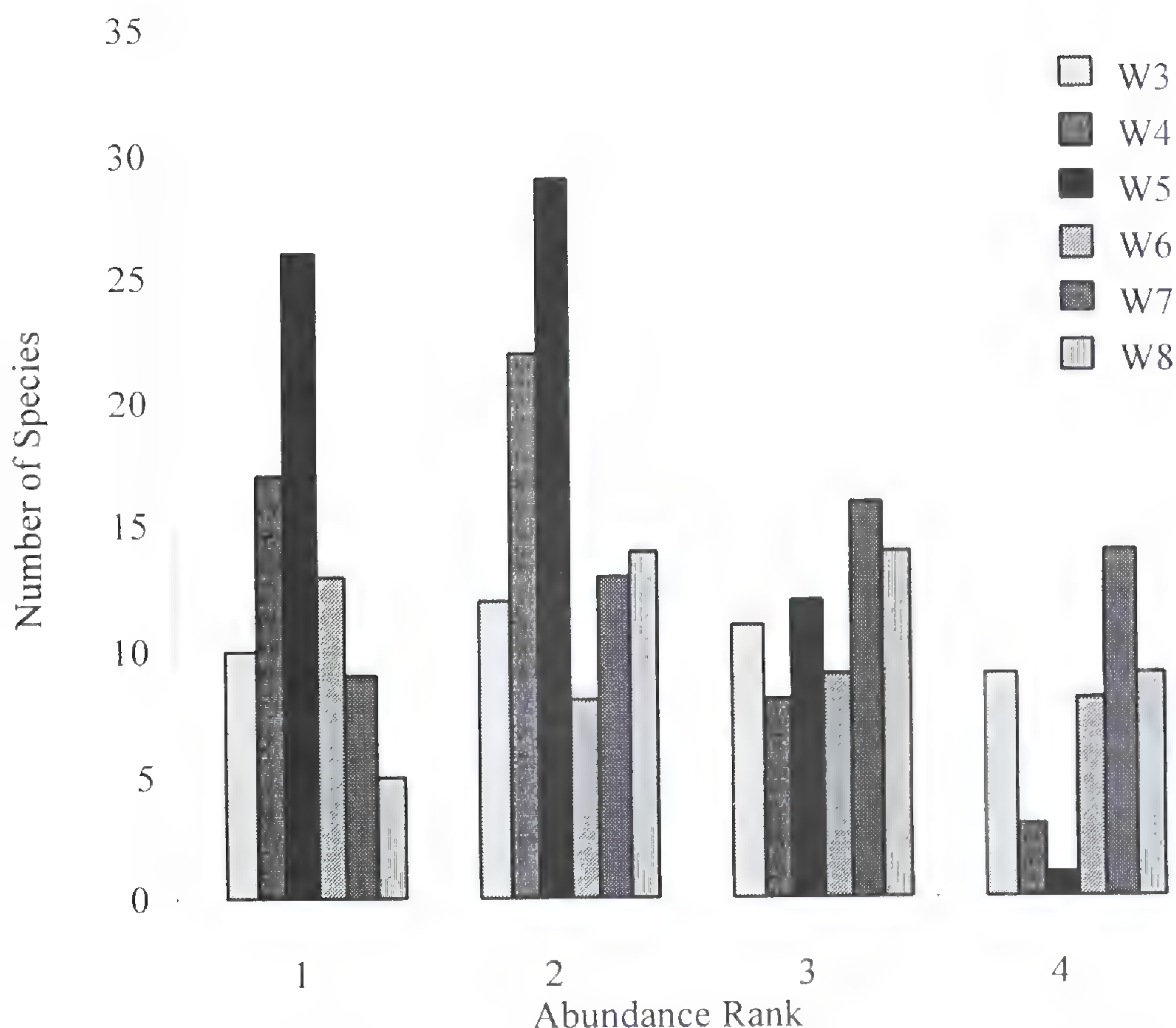


Figure 4. Abundance rank distributions of the herbaceous community in hardwood portions of the watersheds.

successional ages, immigration pool opportunities, and habitat heterogeneity.

Watershed 4 is ten years older than W5 in successional age. Its dense canopy of *Prunus pensylvanica* had largely occluded light from the forest floor, a state witnessed by both the lower occurrence and abundance of shade-intolerant herbaceous species in its flora. According to theoretical expectations, W4 may have experienced a drop in species richness as the result of a transition taking place between the shade-intolerant species, which had dominated since the site was first cleared, and the woodland herbaceous species, which will persist through further canopy development (Bormann and Likens 1979). In contrast, W5's flora was still marked by a higher number of sun-loving, nonwoodland herbaceous species surviving in its less-mature canopy conditions.

It is also possible that W5's richer initial "source pool" for nonwoodland species (namely the adjacent W4, which had been

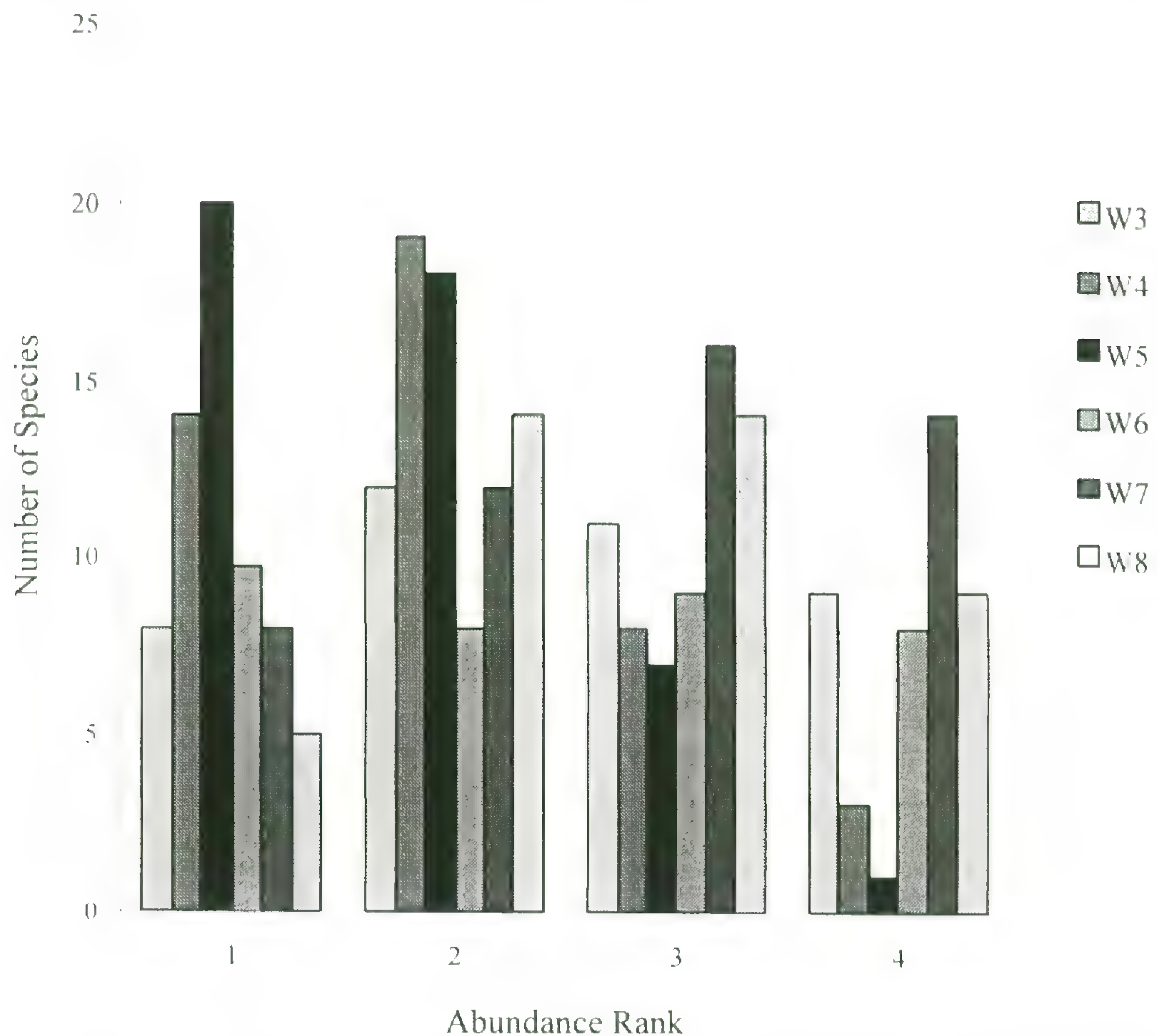


Figure 5. Abundance rank distributions of the woodland herbaceous flora in hardwood portions of the watersheds.

cleared ten years earlier) allowed W5 to develop a richer flora of shade-intolerants in the earliest stages of its succession than W4 (MacArthur and Wilson 1963). All but two of the nonwoodland species found in W4 were also found in W5 (*Festuca ovina* and *Lactuca hirsuta*). Situated as it was between the heavily forested W6 and W5 at the time of its clearing, it seems unlikely that W4 would have had access to the same source pool of shade-intolerant propagules, and so, its early flora may have been poorer than W5's even initially.

Lastly, the differences between the floras of W4 and W5 may be more an inherent factor of the watersheds themselves than any factor of treatment. W5's relatively high habitat diversity may well have resulted in a richer flora than that of W4, even before their treatments. It should be noted that since floristic inventories of W4 and W5 were not conducted before their experimental

clearings, it is impossible to know the level of similarity between their original floras.

Floristic comparisons between the watersheds were further examined by vegetation class, where area was once again found to be insignificant by ANCOVA testing (Table 5). Our initial investigation explored the viability of using tree species data alone to represent HBEF vegetation. While the seven watersheds followed the same rank order in tree species richness as was seen in total species richness, no statistically significant results were produced in the analyses using tree species data alone. No significant relationships were detected between tree species richness and watershed, nor between tree species richness and vegetation class. Combined, these two variables encompassed such inherent site factors as soils, moisture gradients, aspect, treatment history, and habitat diversity. In contrast, these factors were found to be significantly related to total species richness, herbaceous species richness, woodland herbaceous species richness, and nonwoodland herbaceous species richness. This disparity both reflects the reality that New England hardwood and mixed hardwood–spruce–fir forests are composed predominantly of herbaceous species (Bormann and Likens 1979; Kimmins 1997; Westveld et al. 1956), and suggests the possibility that herbaceous species possess an increased sensitivity to aspects of their physical environment relative to woody taxa (Bratton 1976; Carbonneau 1986; Meier et al. 1995; Whitney 1991; Whitney and Foster 1988).

The concept that tree species and herbaceous species recovery from disturbance might be dissimilar is supported by a small body of published research (Crozier and Boerner 1984; Meier et al. 1995; Peterken and Game 1984), but the subject is very much in need of further scientific attention. The forest's herbaceous species differ in a number of ways from trees and shrubs. The most basic differences of scale, which can affect life span, growth and reproduction rates, seed dispersal ranges, rooting breadths, and population-to-area ratios (which lend the increased risk of local extinction), as well as greater reliance on forest floor qualities and microclimate (Bratton 1976; Carbonneau 1986; Meier et al. 1995; Whitney 1991; Whitney and Foster 1988), suggest that herbaceous species may be more impacted by certain forms of disturbance than are woody species. Reliance on tree data alone should therefore be avoided when inferring larger patterns of forest disturbance or recovery.

Tukey's comparison testing (Table 6) revealed that W6, the watershed generally regarded as best representing mature HBEF vegetation, actually represented the low end diversity extreme of the seven watersheds tested. However, W6's flora had a number of unique woodland species (among them *Botrychium oneidense*, *Panax trifolius*, and *Platanthera orbiculata*) as well as markedly abundant populations of most species. Such evidence supports previous studies, which have suggested that this watershed may represent one of the most stable ecosystems examined in this study, nearing or at floristic equilibrium (Bormann et al. 1970; Leak 1987; Whittaker et al. 1974).

Comparison testing also helped identify a critical difference between the highly diverse floras of W5 and W7. While both these watersheds contained significantly richer total and herbaceous floras than W6 (the low-end diversity extreme), W5's flora was not found to be significantly different than W6's in woodland herbaceous species comparisons. This result indicates that, while the flora of W5 was relatively diverse in herbaceous species overall, this diversity is not reflected in the woodland component. As further verification, the flora of W5 was found to be significantly richer than all the other watersheds in nonwoodland species. Thus, W5's diversity can be attributed to the influx of shade-intolerant species that invaded when the watershed was cleared, many of which will not survive further canopy development, while W7's flora is diverse in forest-adapted species.

The apparent similarity between W4's and W6's significantly depauperate woodland floras is also misleading (Table 6). Both watersheds were identified as significantly less rich than W7 (the high end diversity extreme), thereby marking them both as low end diversity extremes. But, it should be recalled that the flora of W6 is significantly depauperate overall, while that of W4 is the third richest watershed in the study. Reviewed in that perspective, W4's overall diversity must also be attributable to the shade-intolerant herbaceous species persisting in its flora. Its significant lack of woodland species seems likely to be a factor of successional age and/or treatment history but, as previously stated, conclusions are difficult to draw as no inventory of W4 was available from before its treatment.

The investigation of species abundance rank distributions again revealed the importance of herbaceous species in assessing overall floristic trends. While tree species abundance did not signifi-

cantly differ across the watersheds, abundance of herbaceous and woodland herbaceous populations was heterogeneous across the hardwood regions of the watersheds (as these are nested data sets, most of the significance in the herbaceous analysis is probably attributable to differences in the woodland herbaceous flora). Since removal of W4, W5, or W7 from the woodland analysis resulted in a loss of significance, it can be inferred that it is these three watersheds that differed significantly from one another in some combination, or combinations. As Figure 5 revealed, W4 and W5 shifted towards the low abundance end of the ranked scale, while W7 is shifted towards the high end. Thus, these significant differences must lie between W7 and the treatment watersheds. Clearly then, W4's and W5's skewed distributions indicate a trend toward smaller population sizes of woodland herbaceous species than those found in reference areas, and significantly smaller populations than those found in W7 (the high-end extreme).

Watersheds with a high percentage of their species in low abundance may possess a high degree of habitat heterogeneity, where the pattern may be reflecting the presence of numerous small microhabitats. Both W5 and W7 encompassed a number of distinct niches not found in the other watersheds of this study. For instance, only these two watersheds possessed well-developed wetland communities (with distinctly different floras). Alternatively, such a pattern may be indicative of a flora with active directional changes taking place. MacArthur and Wilson (1963) defined biological equilibrium as the point at which species immigrations equaled species extinctions. Low population size may indicate a species newly immigrated, or soon to be extirpated from an area. Hence, a flora with a large number of these types of populations may be at floristic disequilibrium, or undergoing an active floristic transition of some kind. Certainly, the early successional floras of W4 and W5 can be characterized in this way.

While species richness was clearly higher for the two clearcut watersheds in the early stages of recovery, the additional species in both cases appeared to be shade-intolerant herbaceous species, most of which will be unlikely to survive further canopy development. In contrast, the population sizes of woodland herbaceous species in these disturbed watersheds were notably lower than reference populations, a condition particularly noteworthy in the

case of W4, whose woodland flora was found to be significantly depauperate as well. Without inventories of these watersheds from before their treatments, it is impossible to know whether these floristic differences are the result of mechanized logging treatments, successional age differences, and/or intrinsic site differences.

There is a great need for floristic studies of New England forests that employ total inventories. Without studies that include detailed herbaceous community data, the possible decline or extirpation of "sensitive" species, rates of exotic species invasion, and effects of timbering, fragmentation, pollution, and other human disturbance on species diversity cannot be accurately assessed. The initial impact of disturbance, as well as the time required to recover stable population sizes, is likely different for the herbaceous and tree communities. Current timber rotation times are based only on tree species recovery, yet it is typically the herbaceous community that most strongly influences diversity overall. Such differences must be addressed, and gaps in our knowledge bridged, if floristic diversity is to be conserved over the long term in New England forests.

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APPENDIX

CHECKLIST OF THE VASCULAR FLORAS OF THE SEVEN HUBBARD
BROOK EXPERIMENTAL WATERSHEDS

Nomenclature conforms to Kartesz (1994). Non-native species are indicated by an asterisk (*). Woodland herbaceous species are indicated by a cross (+). Watersheds on the south to southeastern-facing slope are represented by W1, W3, W4, W5, and W6, while W7 and W8 represent watersheds on the north-facing slope.

	W1	W3	W4	W5	W6	W7	W8
PTERIDOPHYTA							
DENNSTAEDTIACEAE							
+ <i>Dennstaedtia punctilobula</i> (Michx.) Moore	×	×	×	×	×	×	×
DRYOPTERIDACEAE							
+ <i>Athyrium filix-femina</i> (L.) Roth					×	×	×
+ <i>Dryopteris</i> × <i>boottii</i> (Tuck.) Underw.						×	×
+ <i>Dryopteris campyloptera</i> Clarkson				×		×	×
+ <i>Dryopteris carthusiana</i> (Vill.) H. P. Fuchs	×	×	×	×	×	×	×
<i>Dryopteris intermedia</i> (Muhl. ex Willd.) A. Gray	×	×	×	×	×	×	×
+ <i>Gymnocarpium dryopteris</i> (L.) Newman						×	×
+ <i>Onoclea sensibilis</i> L.		×	×	×		×	
+ <i>Polystichum acrostichoides</i> (Michx.) Schott			×				×
EQUISETACEAE							
+ <i>Equisetum arvense</i> L.			×			×	
+ <i>Equisetum sylvaticum</i> L.				×			

APPENDIX

Continued.

	W1	W3	W4	W5	W6	W7	W8
LYCOPODIACEAE							
+ <i>Huperzia lucidula</i> (Michx.) Trevis.	×	×	×	×	×	×	×
+ <i>Lycopodium annotinum</i> L.		×					
+ <i>Lycopodium clavatum</i> L.			×	×		×	×
+ <i>Lycopodium obscurum</i> L.	×	×	×	×		×	×
OPHIOGLOSSACEAE							
+ <i>Botrychium oneidense</i> (Gilbert) House					×		
OSMUNDACEAE							
+ <i>Osmunda cinnamomea</i> L.				×		×	×
+ <i>Osmunda claytoniana</i> L.	×	×	×	×	×	×	×
POLYPODIACEAE							
+ <i>Polypodium virginianum</i> L.	×	×				×	
THELYPTERIDACEAE							
+ <i>Phegopteris connectilis</i> (Michx.) Watt	×	×	×	×	×	×	×
+ <i>Thelypteris noveboracensis</i> (L.) Nieuwl.	×	×	×	×	×	×	×
PINOPHYTA (Gymnosperms)							
PINACEAE							
<i>Abies balsamea</i> (L.) P. Mill.	×	×	×	×	×	×	×
<i>Picea rubens</i> Sarg.	×	×	×	×	×	×	×
<i>Pinus strobus</i> L.				×			
<i>Tsuga canadensis</i> (L.) Carrière		×	×	×	×	×	×
TAXACEAE							
<i>Taxus canadensis</i> Marshall			×		×		
MAGNOLIOPHYTA (Angiosperms)							
MAGNOLIOPSIDA (Dicots)							
ACERACEAE							
<i>Acer pensylvanicum</i> L.	×	×	×	×	×	×	×
<i>Acer rubrum</i> L.	×	×	×	×	×	×	×
<i>Acer saccharum</i> Marshall	×	×	×	×	×	×	×
<i>Acer spicatum</i> Lam.	×	×	×	×	×	×	×
ARALIACEAE							
+ <i>Aralia hispida</i> Vent.				×			
+ <i>Aralia nudicaulis</i> L.	×	×	×	×	×	×	×
+ <i>Aralia racemosa</i> L. subsp. <i>racemosa</i>	×		×	×			
+ <i>Panax trifolius</i> L.					×		
ASTERACEAE							
<i>Anaphalis margaritacea</i> (L.) Benth. & Hook. f.				×			

APPENDIX

Continued.

	W1	W3	W4	W5	W6	W7	W8
+ <i>Aster acuminatus</i> Michx.	×	×	×	×	×	×	×
<i>Aster lateriflorus</i> (L.) Britton			×	×			
+ <i>Aster macrophyllus</i> L.	×						
<i>Euthamia graminifolia</i> (L.) Nutt.			×	×		×	
* <i>Hieracium aurantiacum</i> L.				×		×	
* <i>Hieracium caespitosum</i> Dumort.			×	×			
<i>Hieracium scabrum</i> Michx.				×			
<i>Lactuca hirsuta</i> Muhl. ex Nutt. var.							
<i>sanguinea</i> (Bigelow) Fernald			×				
+ <i>Prenanthes altissima</i> L.	×	×	×	×	×	×	×
+ <i>Senecio aureus</i> L.				×			
<i>Solidago canadensis</i> L.							
var. <i>canadensis</i>			×	×			
+ <i>Solidago macrophylla</i> Pursh	×	×	×	×	×	×	×
<i>Solidago rugosa</i> P. Mill.							
subsp. <i>rugosa</i> var. <i>rugosa</i>	×	×	×	×		×	
* <i>Taraxacum officinale</i> (L.)							
G. H. Weber ex F. H. Wigg.				×			
BALSAMINACEAE							
+ <i>Impatiens capensis</i> Meerb.						×	
BETULACEAE							
<i>Betula alleghaniensis</i> Britton	×	×	×	×	×	×	×
<i>Betula cordifolia</i> Regel	×	×	×	×	×	×	×
<i>Betula papyrifera</i> Marshall	×	×	×	×		×	×
<i>Betula populifolia</i> Marshall		×	×	×		×	×
<i>Ostrya virginiana</i> (P. Mill.) K.							
Koch						×	
CAMPANULACEAE							
<i>Lobelia inflata</i> L.				×			
CAPRIFOLIACEAE							
<i>Diervilla lonicera</i> P. Mill.			×	×			
<i>Lonicera canadensis</i> Bartram							
ex Marshall	×	×	×	×	×	×	×
<i>Sambucus racemosa</i> L.							
subsp. <i>pubens</i> (Michx.) House							
var. <i>pubens</i> (Michx.) Koehne	×	×	×	×	×	×	×
<i>Viburnum alnifolium</i> Marshall	×	×	×	×	×	×	×
CLUSIACEAE							
* <i>Hypericum perforatum</i> L.				×			
CORNACEAE							
<i>Cornus alternifolia</i> L. f.	×	×	×	×	×	×	
+ <i>Cornus canadensis</i> L.	×	×	×	×	×	×	×

APPENDIX

Continued.	W1	W3	W4	W5	W6	W7	W8
DROSERACEAE							
<i>Drosera rotundifolia</i> L.				×			
ERICACEAE							
+ <i>Gaultheria hispidula</i>							
(L.) Muhl. ex Bigelow							×
<i>Vaccinium angustifolium</i> Aiton						×	
<i>Vaccinium myrtilloides</i> Michx.					×	×	×
FAGACEAE							
<i>Fagus grandifolia</i> Ehrh.	×	×	×	×	×	×	×
FUMARIACEAE							
+ <i>Dicentra canadensis</i> (Goldie)							
Walp.		×					
GROSSULARIACEAE							
<i>Ribes cynosbati</i> L.	×	×		×			
<i>Ribes glandulosum</i> Grauer	×	×	×	×	×	×	×
LAMIACEAE							
+ <i>Scutellaria lateriflora</i> L.						×	
MONOTROPACEAE							
+ <i>Monotropa uniflora</i> L.	×	×	×	×	×	×	×
OLEACEAE							
<i>Fraxinus americana</i> L.	×	×	×	×	×	×	×
ONAGRACEAE							
+ <i>Circaea alpina</i> L.						×	
<i>Epilobium coloratum</i> Biehler				×			
OROBANCHACEAE							
+ <i>Epifagus virginiana</i> (L.) W. Bar-							
tram	×	×	×		×		
OXALIDACEAE							
+ <i>Oxalis montana</i> Raf.	×	×	×	×	×	×	×
<i>Oxalis stricta</i> L.				×			
POLYGONACEAE							
<i>Polygonum cilinode</i> Michx.	×	×					
PORTULACACEAE							
+ <i>Claytonia caroliniana</i> Michx.							
var. <i>caroliniana</i>				×		×	
PRIMULACEAE							
+ <i>Trientalis borealis</i> Raf.	×	×	×	×	×	×	×

APPENDIX

Continued.

	W1	W3	W4	W5	W6	W7	W8
RANUNCULACEAE							
+ <i>Actaea pachypoda</i> Elliott		×	×				
+ <i>Anemone quinquefolia</i> L.		×					
+ <i>Coptis trifolia</i> (L.) Salisb. subsp. <i>groenlandica</i> (Oeder) Hultén	×		×	×		×	×
+ <i>Thalictrum pubescens</i> Pursh				×			×
ROSACEAE							
<i>Amelanchier bartramiana</i> (Tausch) M. Roem.				×		×	
<i>Fragaria virginiana</i> Duchesne				×			
<i>Potentilla simplex</i> Michx.				×			
<i>Prunus pensylvanica</i> L. f.	×	×	×	×		×	×
<i>Rubus elegantulus</i> Blanch.	×	×	×	×		×	×
+ <i>Rubus hispidus</i> L.				×			
<i>Rubus idaeus</i> L. subsp. <i>strigosus</i> (Michx.) Focke	×	×	×	×	×	×	×
+ <i>Rubus pubescens</i> Raf.						×	×
<i>Sorbus americana</i> Marshall	×	×	×	×	×	×	×
<i>Spiraea alba</i> Du Roi var. <i>latifolia</i> (Aiton) Dippel				×		×	
<i>Spiraea tomentosa</i> L.				×	×		
RUBIACEAE							
+ <i>Galium asprellum</i> Michx.		×	×	×	×	×	
+ <i>Galium triflorum</i> Michx.			×				
+ <i>Mitchella repens</i> L.	×	×	×	×	×	×	×
SALICACEAE							
<i>Populus grandidentata</i> Michx.				×			
<i>Populus tremuloides</i> Michx.			×	×			
<i>Salix bebbiana</i> Sarg.		×	×	×			
<i>Salix discolor</i> Muhl.				×			
<i>Salix humilis</i> Marshall				×			
SAXIFRAGACEAE							
+ <i>Chrysosplenium americanum</i> Schwein. ex Hook.					×		
+ <i>Tiarella cordifolia</i> L.						×	
SCROPHULARIACEAE							
+ <i>Chelone glabra</i> L.				×		×	
VIOLACEAE							
+ <i>Viola macloskeyi</i> F. E. Lloyd subsp. <i>pallens</i> (Banks ex DC.) M. S. Baker	×	×	×	×	×	×	×
+ <i>Viola rotundifolia</i> Michx.	×	×		×	×	×	×

APPENDIX

Continued.

	W1	W3	W4	W5	W6	W7	W8
LILIOPSIDA (Monocots)							
ARACEAE							
+ <i>Arisaema triphyllum</i> (L.) Schott subsp. <i>triphyllum</i>	×	×	×	×			
CYPERACEAE							
+ <i>Carex arctata</i> W. Boott ex Hook.	×	×	×	×	×	×	×
+ <i>Carex brunnesens</i> (Pers.) Poir.	×	×	×	×		×	×
+ <i>Carex communis</i> Bailey	×		×	×			
+ <i>Carex deflexa</i> Hornem.	×	×	×				
+ <i>Carex gynandra</i> Schwein.		×	×	×	×	×	×
+ <i>Carex intumescens</i> Rudge	×	×	×	×	×	×	×
+ <i>Carex leptonervia</i> (Fernald) Fernald	×		×		×	×	×
+ <i>Carex lurida</i> Wahlenb.				×			
+ <i>Carex scabrata</i> Schwein.				×		×	
<i>Carex scoparia</i> Schkuhr ex Willd.	×		×	×		×	
<i>Scirpus atrocinctus</i> Fernald				×			
<i>Scirpus atrovirens</i> Willd.				×			
<i>Scirpus cyperinus</i> (L.) Kunth		×	×	×		×	
JUNCACEAE							
<i>Juncus brevicaudatus</i> (Engelm.) Fernald				×		×	
<i>Juncus effusus</i> L.							
<i>Juncus tenuis</i> Willd.				×			
LILIACEAE							
+ <i>Clintonia borealis</i> (Aiton) Raf.	×	×	×	×	×	×	×
+ <i>Erythronium americanum</i> Ker Gawl.	×	×	×	×	×	×	×
+ <i>Maianthemum canadense</i> Desf.	×	×	×	×	×	×	×
+ <i>Medeola virginiana</i> L.	×	×	×	×	×	×	×
+ <i>Polygonatum pubescens</i> (Willd.) Pursh	×	×	×	×			
+ <i>Smilacina racemosa</i> (L.) Desf.	×	×	×	×	×	×	×
+ <i>Streptopus amplexifolius</i> (L.) DC.						×	×
+ <i>Streptopus roseus</i> Michx.	×	×	×	×	×	×	×
+ <i>Trillium erectum</i> L.	×	×	×	×	×	×	×
+ <i>Trillium undulatum</i> Willd.	×	×	×	×	×	×	×
+ <i>Uvularia sessilifolia</i> L.	×	×	×	×	×	×	×
+ <i>Veratrum viride</i> Aiton						×	
ORCHIDACEAE							
+ <i>Corallorhiza maculata</i> (Raf.) Raf.			×				×
+ <i>Cypripedium acaule</i> Aiton		×				×	×

APPENDIX

Continued.

	W1	W3	W4	W5	W6	W7	W8
+ <i>Goodyera repens</i> (L.) R. Br. ex Aiton f.							
+ <i>Platanthera orbiculata</i> (Pursh) Lindl.					×		
POACEAE							
<i>Agrostis scabra</i> Willd.	×		×	×			
<i>Agrostis gigantea</i> Roth			×	×			
+ <i>Brachyelytrum septentrionale</i> (Babel) G. C. Tucker	×	×		×		×	
<i>Calamagrostis canadensis</i> (Michx.) P. Beauv. var. <i>canadensis</i>				×			
+ <i>Cinna latifolia</i> (Trevir ex R. Goebb.) Griseb.	×	×	×	×	×	×	
<i>Danthonia compressa</i> Austin ex Peck			×	×			×
<i>Danthonia spicata</i> (L.) F. Beauv. ex Roem. & Schult.		×	×				
<i>Deschampsia cespitosa</i> (L.) P. Beauv.						×	
* <i>Festuca ovina</i> L.			×				
<i>Glyceria melicaria</i> (Michx.) F. T. Hubb.						×	
<i>Glyceria striata</i> (Lam.) Hitchc.				×			
<i>Panicum lanuginosum</i> Elliott var. <i>fasciculatum</i> (Torr.) Fernald		×		×	×		

COMPOSITION, STRUCTURE, AND DYNAMICS OF VEGETATION IN FIFTEEN BEAVER-IMPACTED WETLANDS IN WESTERN MASSACHUSETTS

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ABSTRACT. Quantitative investigations of vegetational composition and structure in 15 beaver-impacted wetlands in Franklin and Hampshire Counties, Massachusetts, were conducted between 1980 and 1995. Four wetland types were identified based on species composition. Five distinctive physiographic zones, each with a characteristic assemblage of plant species, and three successional pathways were observed in the study sites. While soil moisture is clearly a strong influence on plant community structure and composition in beaver-impacted wetlands, hydrological dynamics including frequency, duration, and extent of flooding appear more influential than depth to water table.

Key Words: Beaver (*Castor canadensis*), hydrology, wetland succession, Massachusetts

In the seventy-five years since its return to Massachusetts, the beaver (*Castor canadensis*) has reestablished itself as an important member of the state's fauna and as a powerful force in shaping the region's landscape. In some areas of western Massachusetts nearly every small stream is inhabited, and beavers are increasingly colonizing larger streams as well as rivers, ponds, and lakes.

Foraging activities of the beaver remove large amounts of woody vegetation and thus influence forest composition and structure (Hall 1960; Rutherford 1955). Dam construction alters many aspects of hydrology in the riparian zone including stream velocity, sediment transport, and soil and water chemistry (Naiman et al. 1988; Smith et al. 1991).

Occupation of a site by beavers may continue for a number of years, but eventually a colony will either migrate to another site as food supply dwindles or will be removed by trapping, natural predation, or disease. Even as an unmaintained beaver dam deteriorates, it continues to impound water, especially following spring meltout or heavy precipitation events during the growing

season. Many abandoned beaver dams thus influence stream hydrology for years, even decades, following abandonment. Old dams, lodges, food caches, and channels provide topographic complexity which, when combined with temporal fluctuations in water level, contribute to a particularly rich vascular flora in abandoned beaver wetlands in terms of both species richness and the presence of uncommon and rare species (McMaster and McMaster 2000).

Plant succession in freshwater wetlands has long been a subject of interest to ecologists. Weaver and Clements (1938), Oosting (1956), and others describe a predictable sequence of vegetation types from aquatics to emergents to shrubs and trees, ultimately leading to a relatively stable terrestrial community. The presence of many forested wetlands in the glaciated northeastern United States, particularly those dominated by *Acer rubrum* L. and/or a few other tree species capable of tolerating saturated soils (Golet et al. 1993), suggests that wetland succession in the region is more complex than previously thought, and may be influenced by topographic and geologic factors. Beaver activity may be yet another factor influencing both short-term and long-term wetland succession in the region.

This study was begun by Nancy D. (Mosher) McMaster in 1980. She initially sampled all sites from 1980–1984 and began resampling in 1985 (McMaster 1989). Upon her death in 1990, Robert T. McMaster resumed the sampling schedule, employing the transects and methodology of the previous work. This paper presents classifications of the 15 western Massachusetts study sites and the plant communities they support, a model of plant succession, and an analysis of factors influencing vegetation structure and dynamics in beaver-impacted wetlands.

MATERIALS AND METHODS

Study sites. The 15 study sites are located on first and second-order streams on the eastern slope of the Berkshire Plateau in Franklin and Hampshire Counties, Massachusetts (Table 1). Sites range in area from 0.6 to 8.0 ha and in elevation from 164 to 465 m above sea level.

Previous to the reintroduction of beavers in western Massachusetts in the 1920s, all study sites were upland bordering a narrow stream course. Two sites are referred to as “pasture” in

Table 1. County, watershed, elevation above sea level, area, and age since last beaver occupation (as of 1995) for the 15 study sites. ¹Refers to the Mill River with headwaters in Conway and which enters the Connecticut River at Hatfield. ²Refers to the Mill River with headwaters in Goshen and Ashfield and which enters the Connecticut River at Easthampton. Reprinted from McMaster and McMaster (2000).

Site	County	Watershed	Eleva- tion (m)	Area (ha)	Age (years)
Ashfield 1	Franklin	Westfield River	417	3.8	20
Ashfield 2	Franklin	Westfield River	417	1.4	40
Ashfield 3	Franklin	Westfield River	393	2.5	1
Ashfield 4	Franklin	Mill River ¹	453	6.2	1
Ashfield 5	Franklin	Mill River ¹	453	2.5	1
Ashfield 6	Franklin	Deerfield River	465	1.8	16
Conway 1	Franklin	Mill River ¹	369	1.8	25
Conway 2	Franklin	Mill River ¹	362	2.5	35
Conway 3	Franklin	Mill River ¹	338	3.2	18
Conway 4	Franklin	Mill River ¹	329	1.0	15
Conway 5	Franklin	Mill River ¹	243	3.5	16
Goshen 1	Hampshire	Mill River ²	417	2.1	18
Williamsburg 1	Hampshire	Mill River ¹	220	7.8	26
Williamsburg 2	Hampshire	Mill River ²	164	0.6	16
Worthington 1	Hampshire	Westfield River	375	8.0	10

old deeds; a narrow cart road dating to at least the mid-nineteenth century crosses one site; stone walls dissect four sites; submerged stumps and standing dead trees, mostly of *Pinus strobus* L., *Tsuga canadensis* Carrière, *Picea rubens* Sarg., and *P. abies* (L.) Karst, are present in eight sites (McMaster 1989). All sites have a history of beaver occupation but were unoccupied when first sampled. Details of site selection may be found in McMaster and McMaster (2000); vegetation maps of each site may be found in McMaster (1997).

Site histories were reconstructed by examination of U.S.D.A. Soil Conservation Service maps and panchromatic black and white aerial photographs (scale 1:24,000), U.S. Geological Survey maps, deeds, town histories, by communication with property owners, and by field observation. Sites were monitored regularly for presence or absence of active beaver colonies throughout the period of the study. Site age (i.e., number of years since last beaver occupation; when a site is reoccupied, its age becomes

zero) was determined from communication with property owners or local residents and from direct observation.

Vegetation sampling. Transects were established across each site parallel to the abandoned beaver dam. Each transect was placed within a zone of relatively homogeneous vegetation based upon life form of the dominant vegetation. Transects extended across the wetland to the upland margin on each side of a site. Number of transects per site ranged from 3 to 9 depending on the size and complexity of the site.

Along each transect, 0.5 m $\times$ 0.5 m quadrats were located at 2 m intervals. Number of quadrats per transect ranged from 6 to 74 (mean = 24.4). Within each quadrat, percent cover was determined by visual estimate for all vascular plants and for those nonvascular plants with cover $> 1\%$.

All sites were originally sampled in midsummer between 1980 and 1984 (McMaster 1989; Mosher 1981). Three sites (Conway 1, 2, and 3) were resampled at five-year intervals. The remaining 12 sites were to be resampled at ten-year intervals when possible. Seven of these were resampled on schedule. Ashfield 3, which had been reoccupied by beavers in 1992, was resampled in 1993 after the site was once again abandoned. Four sites originally sampled in 1984 (Ashfield 6, Conway 5, Goshen 1, and Worthington 1) were not resampled in 1994 or subsequently due to continued beaver occupation which made sampling impractical. All sites were revisited at regular intervals and beaver activity recorded.

Nomenclature for vascular taxa follows Gleason and Cronquist (1991). A complete list of the vascular flora of the 15 sites appears in McMaster and McMaster (2000).

Collection of hydrologic and sediment data. Observation wells of perforated, 1 $\frac{3}{4}$ -inch diameter PVC pipe, 1 m in length, were placed near the midpoint of 33 transects in 10 unoccupied sites, and ground water levels were monitored biweekly from late spring to late fall, 1995. For sites with standing water, staff gauges were monitored biweekly during the summers of 1994 and 1995.

Field analysis of water samples was accomplished in June, 1995, using an Accumet 1002 Field pH Meter for pH [referred to below as pH (field)], a YSI Model 34 Conductance-Resistance

Meter for specific conductance, and a YSI Model 58 Dissolved Oxygen Meter for dissolved oxygen concentration. One 100 ml water sample was collected immediately above the dam at each site in September, 1995, transported to the laboratory, and stored in the dark at 4°C. The Accumet 1002 Field pH Meter was also used to measure pH for these samples, referred to below as pH (lab). Alkalinity of one to three samples from each site was determined by titration with 0.01 M HCl according to the protocol in American Public Health Association (1989).

Depth of organic material was measured using a 2 m graduated steel rod. Number of measurements per transect ranged from 2 to 13 (mean = 6). Depths greater than 2 m were recorded as 2 m and calculations based upon those estimates are noted below.

Data analysis. A modification of the importance value of Mueller-Dombois and Ellenberg (1974) was calculated by summing relative percent cover and relative frequency for each species in all quadrats of a transect and is referred to below as MIV. Sites and transects were ordinated using two-way indicator species analysis (TWINSPAN; Hill 1979). Only species with $MIV \geq 5$ were used in this analysis. Default values were used for all parameters except cut values which were set at 5, 10, 20, and 30. Data were then ordinated with detrended correspondence analysis using the software program CANOCO (ter Braak 1988) including only species with $MIV \geq 5$ in each transect and setting all parameters at default values. Transects identified as outliers were removed and the analysis repeated to permit a more precise ordination of the remaining data as recommended by Gauch (1982).

When a transect was sampled more than once, each resampling was treated as a separate transect for all ordinations. This approach has the advantage of revealing temporal changes in composition. In analyzing the resulting ordination data, however, it must be remembered that resampled transects have greater influence on the ordination than those sampled only once. Similarity coefficients used to compare species composition of sites included those of Jaccard, Ellenberg, Sørensen, Gleason, and Spatz as described in Mueller-Dombois and Ellenberg (1974).

Possible relationships between abiotic parameters and the species composition of vegetation were examined using TWINSPAN and canonical correspondence analysis using the CANOCO software program (ter Braak 1988). Because collection of abiotic data

was completed during the summer of 1995, only vegetation data for the 48 transects in 11 sites sampled during the period 1992–1995 were used for this analysis. Canonical correspondence analysis was employed to examine relationships between species composition and pH, conductivity, alkalinity, dissolved oxygen concentration, depth of organic matter, distance to water table, and site age. Default values were used for all parameters in this analysis. Where data were absent, means for that transect were substituted as recommended in ter Braak (1988).

RESULTS

Site classification. Based on data from the most recent sampling, the 15 study sites were clustered into four groups (I–IV) with TWINSpan. Data for each site and each TWINSpan group are presented in Tables 2 and 3.

Group I included three sites dominated by the shrubs *Alnus incana* and *Spiraea alba* var. *latifolia*. Site age ranged from 16 to 26 years. These sites were characterized by relatively low water table, very low percent cover of *Sphagnum* spp., and high percent cover of trees and shrubs. Cover of tussock-colonizing graminoids was variable, ranging from 1.5 to 54.6%. Depth of organic matter ranged from 65.6 to 113.1 cm (Table 2). This group corresponds to “shrub swamp” as defined by Reschke (1990).

Group II included five sites dominated by tussock-colonizing graminoids *Calamagrostis canadensis* and *Carex stricta* and/or mud flat colonizers *Leersia oryzoides* and *Eleocharis* spp. Site age ranged from 1 to 40 years. Like Group I, these sites were characterized by relatively low water table and low percent cover of *Sphagnum* spp., but with a low percent cover of trees and shrubs, as well. Cover of tussock-colonizing graminoids ranged from 0 to 56.5%. Depth of organic matter ranged from 65.7 to 154.3 cm (Table 2). This group corresponds to “shallow emergent marsh” as defined by Reschke (1990).

Group III included three sites dominated by *Calamagrostis canadensis* or *Typha latifolia* with large areas of standing water usually covered with *Najas flexilis* or *Lemna minor*. Two of the three sites had been abandoned only one year when sampled; one site had been abandoned 16 years. These sites were characterized by high water table, low percent cover of *Sphagnum* spp., and low percent cover of trees and shrubs. Cover of tussock-coloniz-

Table 2. Site age, % cover of trees and shrubs, % cover of tussock-colonizing graminoids, % cover of *Sphagnum* spp., mean depth to water table, and mean depth of organic matter for 15 study sites and four TWINSPAN groups. – Indicates data not available. *Indicates sites with measurements of organic matter > 200 cm (see Materials and Methods). “FL” indicates sites that were flooded in 1995 when water table data were collected. Site abbreviations: Ashfd. = Ashfield; Willb. = Williamsburg; Worth. = Worthington.

Site	Site Age (years ± sem)	% Cover of Trees and Shrubs	% Cover of Tus- sock- Co- lon- izing Gram- inoids	% Cover of <i>Sphag- num</i> spp.	Mean Depth to Water Table (cm ± sem)	Mean Depth of Organic Matter (cm ± sem)
Group I						
Willb. 1	26	52.2	54.6	2.7	13.9 ± 2.2	113.1 ± 9.1*
Willb. 2	16	70.9	8.2	2.7	31.4 ± 3.3	113.1 ± 11.9*
Conway 3	18	38.2	1.5	0.1	7.5 ± 1.4	65.6 ± 5.9
MEAN	20.0 ± 3.1	53.8	21.5	1.8	15.0 ± 1.7	95.4 ± 5.7
Group II						
Ashfd. 6	16	17.4	7.2	0.0	FL	–
Worth. 1	10	14.3	0.0	2.5	FL	–
Ashfd. 1	20	9.9	56.5	2.1	16.1 ± 2.2	154.3 ± 12.8*
Ashfd. 2	40	11.8	47.0	12.0	2.1 ± 0.7	136.5 ± 15.2*
Ashfd. 3	1	1.9	25.9	0.2	14.2 ± 1.7	65.7 ± 4.5
MEAN	17.4 ± 6.5	11.1	27.3	3.4	12.0 ± 1.3	106.7 ± 7.0
Group III						
Ashfd. 4	1	8.7	0.3	0.0	5.6 ± 1.5	89.0 ± 9.4*
Ashfd. 5	1	11.1	35.7	0.3	FL	54.1 ± 5.2
Conway 5	16	30.5	13.9	0.0	FL	–
MEAN	6.0 ± 5.0	16.7	16.6	0.1	5.6 ± 1.5	81.9 ± 7.8
Group IV						
Goshen 1	18	40.1	5.2	1.3	–	–
Conway 4	15	30.1	5.5	15.7	6.1 ± 1.1	46.5 ± 5.0
Conway 1	25	8.3	2.0	26.9	2.4 ± 1.2	84.5 ± 8.3
Conway 2	35	41.0	0.5	35.6	1.8 ± 0.7	189.1 ± 10.9*
MEAN	23.3 ± 8.9	29.9	3.3	19.9	3.4 ± 0.6	94.6 ± 8.9

Table 3. Water chemistry characteristics for 15 study sites and four TWINSPAN groups. Group means include only 11 sites (*) resampled from 1992–1995. – Indicates data not available. See Table 2 for site abbreviations.

Site	pH Lab (± sem)	pH Field (± sem)	Alkalinity (mg/l ± sem)	Conductivity (mhos ± sem)	Dissolved Oxygen Concentration (mg/l ± sem)
Group I					
*Willb. 1	6.10	6.16 ± 0.03	13.0 ± 2.5	63.8 ± 2.4	5.4 ± 1.0
*Willb. 2	6.95	6.36 ± 0.08	27.4 ± 1.8	60.0 ± 0.0	9.5 ± 0.3
*Conway 3	6.61	6.40 ± 0.05	21.5 ± 7.5	81.3 ± 1.3	–
MEAN	6.55 ± 0.25	6.34 ± 0.05	20.6 ± 3.4	67.0 ± 2.7	8.0 ± 0.8
Group II					
Ashfd. 6	7.04	6.19 ± 0.20	26.0 ± 7.4	108.3 ± 4.0	3.8 ± 0.6
Worth. 1	5.22	4.84 ± 0.05	2.0 ± 1.5	42.5 ± 7.5	–
*Ashfd. 1	6.96	6.42 ± 0.14	28.1 ± 2.8	166.7 ± 1.7	7.2 ± 0.2
*Ashfd. 2	6.45	6.55 ± 0.00	19.8 ± 4.3	158.3 ± 1.7	7.1 ± 0.3
*Ashfd. 3	5.94	5.76 ± 0.11	1.3 ± 0.3	35.7 ± 0.3	12.7 ± 1.1
MEAN	6.45 ± 0.29	6.28 ± 0.11	18.1 ± 4.8	116.5 ± 17.6	9.1 ± 0.9
Group III					
*Ashfd. 4	6.74	6.40 ± 0.18	33.8 ± 16.8	118.0 ± 13.6	5.6 ± 0.7
*Ashfd. 5	6.16	6.26 ± 0.29	21.0 ± 1.0	150.0 ± 10.0	2.2 ± 1.2
Conway 5	6.53	6.45 ± 0.12	29.3 ± 9.8	111.7 ± 9.3	1.8 ± 0.2
MEAN	6.45 ± 0.29	6.34 ± 0.11	26.1 ± 6.2	116.7 ± 11.1	4.0 ± 0.7
Group IV					
Goshen 1	6.70	6.82 ± 0.30	19.8 ± 1.3	168.0 ± 3.4	3.2 ± 0.5
*Conway 4	6.53	5.22 ± 0.05	17.8 ± 1.3	57.0 ± 1.2	–
*Conway 1	6.40	6.39 ± 0.04	14.5	143.8 ± 2.4	–
*Conway 2	5.64	5.27 ± 0.07	2.8 ± 1.3	45.8 ± 4.0	–
MEAN	6.19 ± 0.28	5.75 ± 0.17	11.1 ± 3.5	79.7 ± 9.6	–

Table 4. Modified importance values (MIV) of *Sphagnum* spp., *Calamagrostis canadensis*, and *Carex stricta* in 11 sites. Sites are arranged in order of increasing pH (lab).

	Site pH (lab)	<i>Sphagnum</i> spp.	<i>Calamagrostis</i> <i>canadensis</i>	<i>Carex</i> <i>stricta</i>
Conway 2	5.64	43.4	0.0	1.3
Ashfield 3	5.94	0.6	27.7	13.0
Williamsburg 1	6.10	5.7	35.3	51.9
Ashfield 5	6.16	0.8	66.8	6.9
Conway 1	6.40	30.9	0.0	2.6
Ashfield 2	6.45	21.1	23.2	71.8
Conway 4	6.53	15.8	0.0	9.2
Conway 3	6.61	0.3	0.0	3.3
Ashfield 4	6.74	0.0	0.0	1.5
Williamsburg 2	6.95	3.2	1.8	8.3
Ashfield 1	6.96	4.2	57.6	53.3

ing graminoids ranged from 0.3 to 35.7%. Depth of organic matter ranged from 54.1 to 89.0 cm (Table 2). This group corresponds to “shallow emergent marsh” as defined by Reschke (1990), but is distinguished from Group II by the presence of large areas of open water colonized by free-floating and submersed aquatic herbs.

Group IV included four sites dominated by *Spiraea alba* var. *latifolia* and/or *Alnus incana*. Site age ranged from 15 to 35 years. These sites were characterized by high water table, generally high percent cover of *Sphagnum* spp., and intermediate tree and shrub cover. Cover of tussock-colonizing graminoids ranged from 0.5 to 5.5%. Depth of organic matter ranged from 46.5 to 189.1 cm (Table 2). This group corresponds to “shrub swamp” as defined by Reschke (1990), but is distinguished from Group I by the abundance of *Sphagnum* spp. in three of four sites.

Groups I, II, and III showed little variation in water chemistry (Table 3). Group IV was much lower in mean pH (field) than Groups I, II, and III, lower in mean alkalinity than groups I and III, and intermediate in mean conductivity between Group I and Groups II and III. Table 4 lists MIVs of three pH-sensitive taxa, *Sphagnum* spp., *Calamagrostis canadensis*, and *Carex stricta*, in the 11 sites sampled since 1992. While an association is suggested between *Sphagnum* spp. and more acidic sites, no clear pattern is observable between pH (lab) and importance values of *Calamagrostis canadensis* and *Carex stricta*.

Table 5. Means of five coefficients of similarity for four pairs of sites < 1 km apart compared to sites ≥ 1 km apart.

Distance between sites (km)	Number of site pairs	Jaccard	Ellenberg	Sørensen	Gleason	Spatz
< 1 km	4	0.43	0.65	0.59	0.79	0.14
≥ 1 km	101	0.31	0.44	0.47	0.60	0.08

Other relationships are also suggested by the TWINSpan ordination of sites (Tables 2 and 3). The three most recently abandoned sites (Ashfield 3, 4, and 5) showed compositional similarities as did two pairs of sites with a common water source, Williamsburg 1 and 2 (on Joe Wright Brook) and Ashfield 1 and 2 (on Stones Brook). Three pairs of geographically proximate sites were clustered together: Ashfield 1 and 2, Ashfield 4 and 5, and Conway 1 and 2. A comparison of means of five coefficients of similarity for pairs of sites < 1 km apart with those for sites ≥ 1 km apart (Table 5) suggests greater floristic similarity among closer sites.

Abiotic characteristics. Differences in mean depth to water table were much greater between sites (Table 2) than between transects within sites (Table 6). No substantial within-site differences were found in 6 of 10 sites. Where large within-site differences did occur, they were usually between the first transect (i.e., the transect closest to the dam) where water levels were highest, and subsequent transects where water levels were lower. The atypical pattern in Conway 3 resulted from the unusual topography of that site: three dams were present in 1995, but only the second dam was impounding water and only transect 3, which lay immediately upstream from the second dam, was affected.

Differences in mean depth of organic matter were also greater between sites (Table 2) than between transects within sites (Table 6). No substantial within-site differences were found in 3 of 11 sites. As with depth to water table, greatest within-site differences usually occurred between the first transect and subsequent transects. The small amount of organic matter immediately above the dam in most sites was probably due to repeated flushing as runoff moved rapidly through the gap in the abandoned dam. The five

sites with the greatest depth of organic sediments were all 16 years or older.

Water chemistry parameters followed a pattern similar to that for depth to water table and depth of organic matter, with larger differences between sites (Table 3) and much smaller differences within sites (Table 6).

Plant community types. One hundred fifty-one transects (including repeat samplings) and 219 species were clustered into five major community types in three hierarchical divisions using TWINSpan (Figure 1). The scatter plot of samples produced by detrended correspondence analysis using the software package CANOCO is shown in Figure 2 with numbers indicating the five community types identified by TWINSpan.

The five transects through standing water (labeled "1" in Figure 2) were removed and the analysis repeated (Figure 3). Comparison of the abiotic characteristics of each site suggests that Axis 1 corresponds to moisture gradient (transects to the right occurring in saturated soils and those to the left in increasingly drained soils) and Axis 2 corresponds to reflooding regime (lower transects are subject to more frequent, extensive, and longer-lasting reflooding than upper transects). Solid lines indicate that the plant communities identified by TWINSpan were ordinated by detrended correspondence analysis into contiguous groups with relatively few outliers.

Each of the five plant communities delineated by TWINSpan may be associated with a distinct physiographic zone within the study sites. Table 7 lists characteristic taxa for each zone (i.e., taxa with high MIVs in that zone and low MIVs in the other zones). Taxa with high MIVs in more than one zone are not included.

Zone 1, open water: *Najas flexilis*–*Utricularia vulgaris* Community

This zone was usually located immediately upstream from the beaver dam, although it sometimes occurred in depressions elsewhere in a site, as well. The zone was often largest in spring and after heavy rainfalls, especially in sites with an intact dam, but was usually reduced in size as summer progressed and in some sites dried up for a few weeks during prolonged drought. Organic sediments were thinnest and dissolved oxygen concentrations were lowest in this zone.

Table 6. Water chemistry characteristics by transect for the 15 study sites and depth to water table and depth of organic matter in unoccupied sites, summer, 1995. – Indicates data not available. *Indicates transects with one or more measurements of organic matter > 200 cm (see Materials and Methods). Numbers of depth measurements for each transect are shown in parentheses. See Table 2 for site abbreviations.

Site	Transect	pH (field)	Alkalinity (mg/l)	Conductivity (mhos)	Dis- solved Oxygen Concentration (mg/l)	Mean Depth of Water Table (cm)	Mean Depth of Organic Matter (cm)
Ashfd. 1	1	6.63	30.5	165	6.9	17.9 (7)	98.6 (7*)
	2	6.47	31.4	165	7.4	–	167.5 (8*)
	3	6.15	–	170	7.3	14.4 (7)	195.0 (7*)
Ashfd. 2	1	6.54	15.5	160	6.6	–	41.9 (8)
	2	6.55	24.0	160	7.3	2.1 (7)	180.0 (9*)
	3	6.55	–	155	7.5	2.0 (7)	188.6 (7*)
Ashfd. 3	1	5.63	1.5	36	10.8	7.0 (9)	31.4 (11)
	2	5.67	1.0	35	12.7	14.6 (9)	79.2 (13)
	3	5.99	–	36	14.6	22.1 (9)	76.4 (11)
	4	–	–	–	–	13.1 (8)	76.3 (8)
Ashfd. 4	1	6.72	17.0	90	5.8	–	42.5 (8)
	2	6.70	50.5	170	3.6	–	47.9 (7)
	3	–	–	110	–	–	66.7 (9)
	4	6.02	–	110	6.8	6.4 (7)	130.9
	5	6.14	–	110	6.1	4.7 (7)	138.8 (8*)
Ashfd. 5	1	6.55	19.0	140	3.4	–	60.0 (3)
	2	5.97	22.5	160	1.0	–	35.0 (3)
	3	–	21.4	–	–	–	52.5 (2)
	4	–	–	–	–	–	68.3 (3)
Ashfd. 6	1	5.89	18.0	110	4.5	–	–
	2	5.77	48.0	110	5.3	–	–
	3	6.06	18.5	110	5.0	–	–
	4	6.33	–	90	2.8	–	–
	5	–	–	110	3.2	–	–
	6	6.88	–	120	1.8	–	–
Conway 1	1	6.47	14.5	140	–	5.3 (4)	38.8 (4)
	2	6.44	–	150	–	0.8 (4)	53.8 (4)
	3	6.35	–	145	–	2.3 (4)	114.1 (7)
	4	6.28	–	140	–	1.5 (4)	98.6 (7)
Conway 2	1	5.21	1.5	35	–	0.3 (4)	200.0 (4*)
	2	5.46	4.0	35	–	0.7 (7)	160.0 (3*)
	3	5.20	–	50	–	2.3 (7)	200.0 (2*)
	4	5.19	–	45	–	2.3 (4)	200.0 (2*)
	5	–	–	60	–	3.3 (4)	–
	6	–	–	50	–	–	–

Table 6. Continued.

Site	Tran- sect	pH (field)	Alka- linity (mg/l)	Con- duc- tivity (mhos)	Dis- solved	Mean Depth of Water Table (cm)	Mean Depth of Organic Matter (cm)
					Oxygen Concen- tration (mg/l)		
Conway 3	1	6.24	14.0	80	—	14.4 (5)	51.1 (9)
	2	6.48	29.0	85	—	2.2 (5)	55.0 (6)
	3	6.43	—	80	—	9.8 (5)	70.8 (6)
	4	6.43	—	80	—	—	82.5 (2)
	5	—	—	—	—	—	108.3 (3)
Conway 4	1	5.15	16.5	55	—	1.3 (4)	43.3 (6)
	2	5.18	19.0	55	—	7.0 (4)	45.0 (5)
	3	5.32	—	60	—	6.8 (4)	53.8 (4)
	4	—	—	55	—	9.3 (4)	45.0 (2)
	5	—	—	60	—	—	—
Conway 5	1	6.15	19.5	120	2.1	—	—
	2	—	39.0	105	2.0	—	—
	3	6.37	—	110	1.4	—	—
	4	—	—	115	1.8	—	—
	5	6.61	—	75	2.6	—	—
	7	6.68	—	145	1.0	—	—
Goshen 1	1	6.51	18.5	160	2.0	—	—
	2	—	21.0	165	2.4	—	—
	3	7.12	—	165	4.8	—	—
	4	—	—	180	2.6	—	—
	5	—	—	170	4.2	—	—
Willb. 1	1	6.17	10.5	70	6.9	6.3 (6)	115.7 (7*)
	2	6.11	15.5	60	7.3	18.1 (7)	107.9 (7)
	3	6.21	—	60	3.7	16.0 (7)	113.3 (6)
	4	—	—	65	3.7	—	115.8 (6)
Willb. 2	1	6.33	25.5	60	9.3	32.8 (4)	100.0 (6*)
	2	6.44	29.0	60	10.2	26.0 (4)	85.0 (5)
	3	6.51	—	60	8.9	34.0 (3)	141.7 (3)
	4	6.15	—	60	9.4	40.0 (1)	146.3 (4)
Worth. 1	1	4.79	0.5	50	—	—	—
	2	4.90	3.5	35	—	—	—

Of the 43 species sampled in Zone 1, floating, submersed, and emergent hydrophytes were the most common life forms. Mats of *Lemna minor*, *Najas flexilis*, and *Utricularia vulgaris* often predominated in deeper water, while stands of *Sparganium an-*

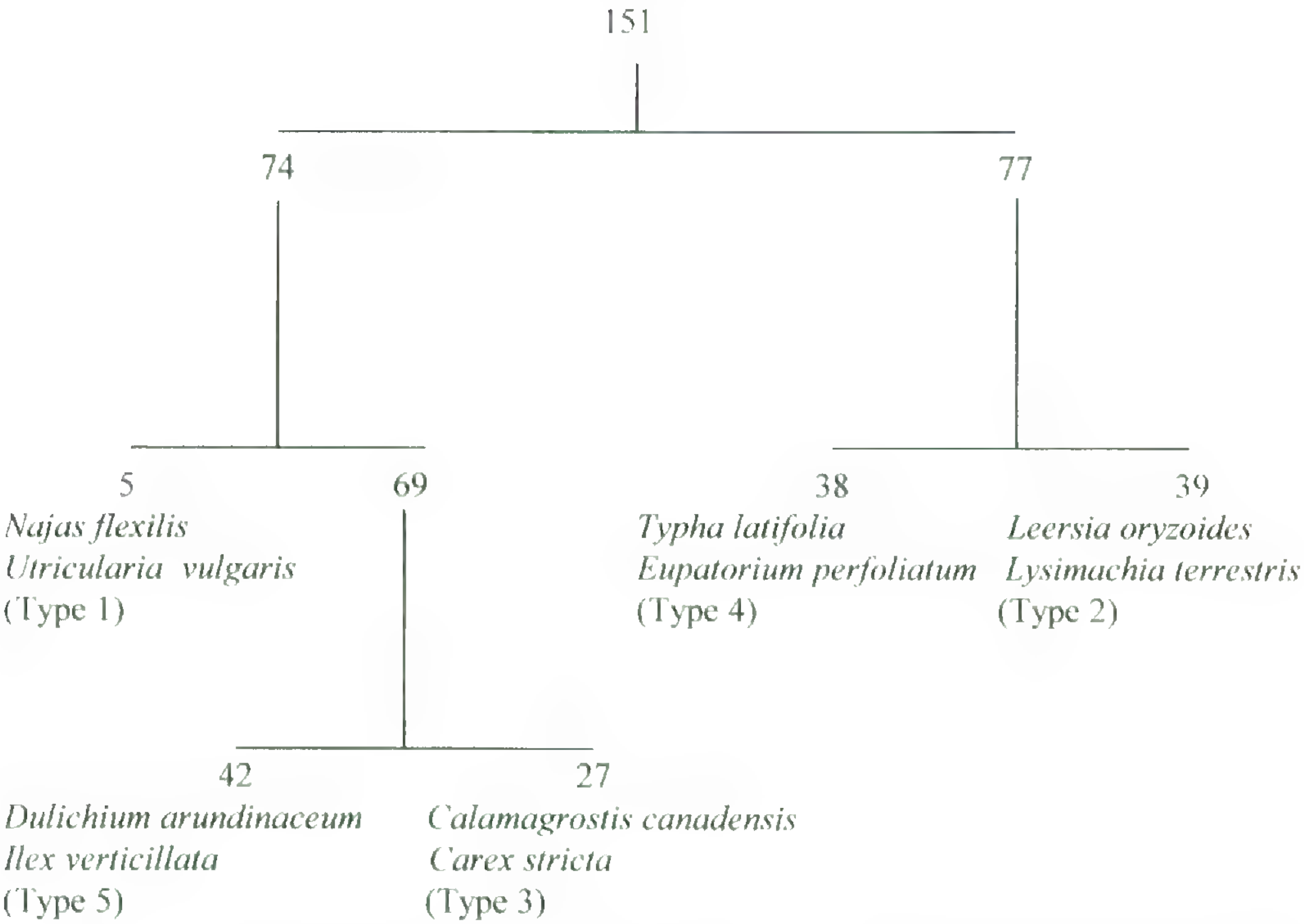


Figure 1. Five major vegetation types in 151 transects as delineated with TWINSpan. Numbers indicate number of transects in each division.

drocladum (Engelm.) Morong occurred in shallower water. Rooted hydrophytes such as *Brasenia schreberi* J. F. Gmel., *Nuphar variegata* Durand, *Polygonum amphibium* L., and *Potamogeton* spp. also occurred, though less frequently, in this zone. Where open water occurred due to reoccupation of a site that had been abandoned for a number of years, some of the pre-existing vegetation persisted, including woody taxa such as *Acer rubrum* and *Spiraea alba* var. *latifolia*, and tussock-colonizing graminoids.

Zone 2, mud flat: *Leersia oryzoides*–*Lysimachia terrestris*
Community

This zone of recently exposed pond bottom sediments occurred immediately upstream from the beaver dam and the open water of Zone 1. It usually attained its maximum extent in late summer and was frequently reflooded during the growing season. The stream often cut a narrow channel through the bottom sediments of this zone, increasing flow and resulting in higher mean dissolved oxygen concentration than in the other zones.

Of the 146 species sampled in Zone 2, emergent hydrophyte was the most common life form. *Leersia oryzoides* was the most

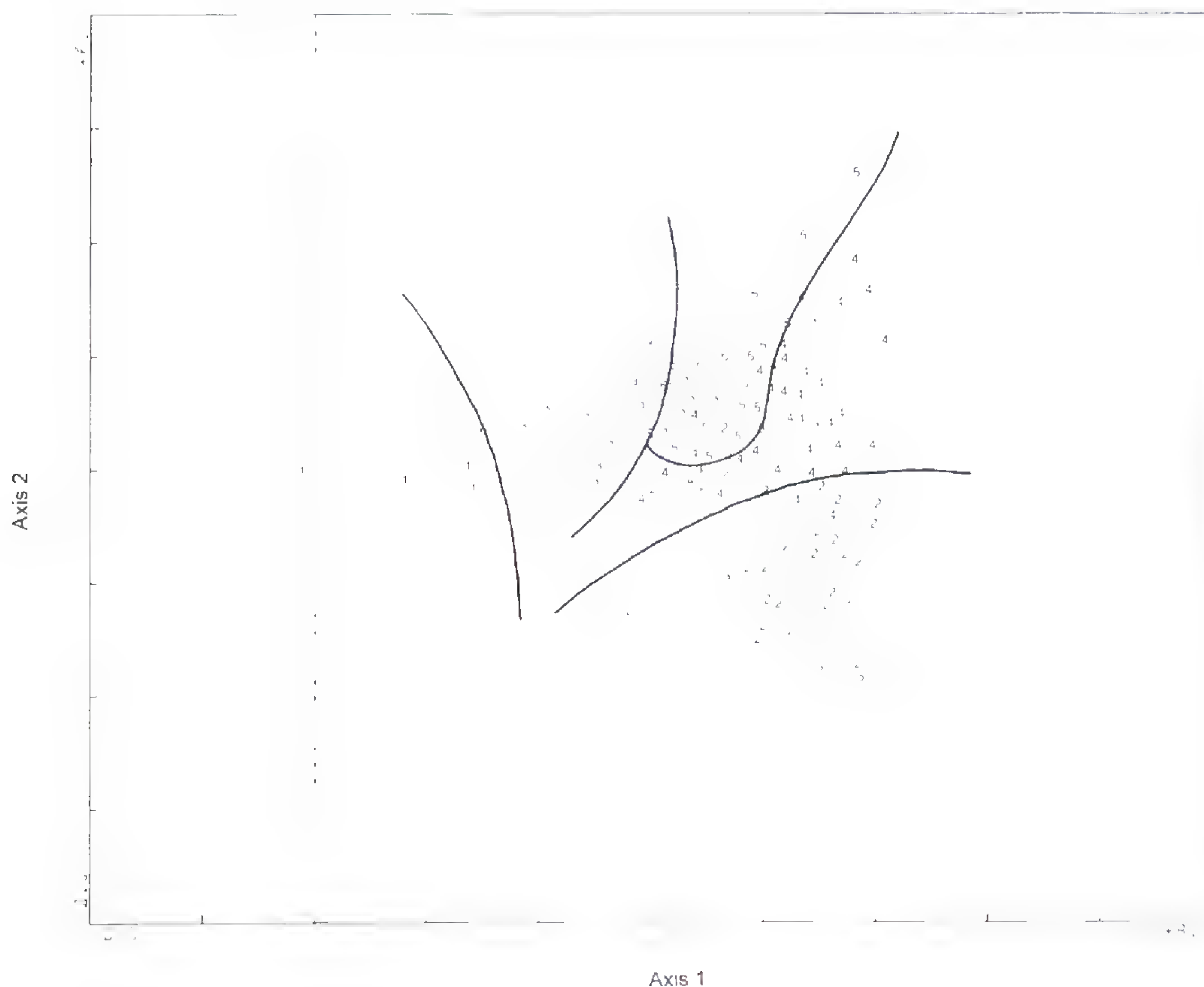


Figure 2. Plot of detrended correspondence analysis sample ordination, Axes 1 and 2, for transects in 15 beaver-impacted wetlands based on modified importance values ≥ 5 . Numbers indicate five community types as identified by TWINSpan: 1 – *Najas flexilis*–*Utricularia vulgaris* Community, 2 – *Leersia oryzoides*–*Lysimachia terrestris* Community, 3 – *Calamagrostis canadensis*–*Carex stricta* Community, 4 – *Typha latifolia*–*Eupatorium perfoliatum* Community, 5 – *Dulichium arundinaceum*–*Ilex verticillata* Community.

important species of this zone in most sites, although *Lysimachia terrestris* was even more important than *L. oryzoides* in a few sites. Other important species included *Agrostis gigantea*, *Eleocharis acicularis*, and *Galium tinctorium*. Taxa sometimes occurring in Zone 2 that may have persisted from before the last re-occupation included *Carex stricta*, *Calamagrostis canadensis*, *Scirpus cyperinus*, *Spiraea alba* var. *latifolia*, and *S. tomentosa*.

Zone 3, wet meadow: *Calamagrostis canadensis*–*Carex stricta* Community

Zone 3 was located farther upstream on soils that were subject to regular fluctuations of the water table. Among the five zones, mean depth of organic sediments was greatest in this zone.

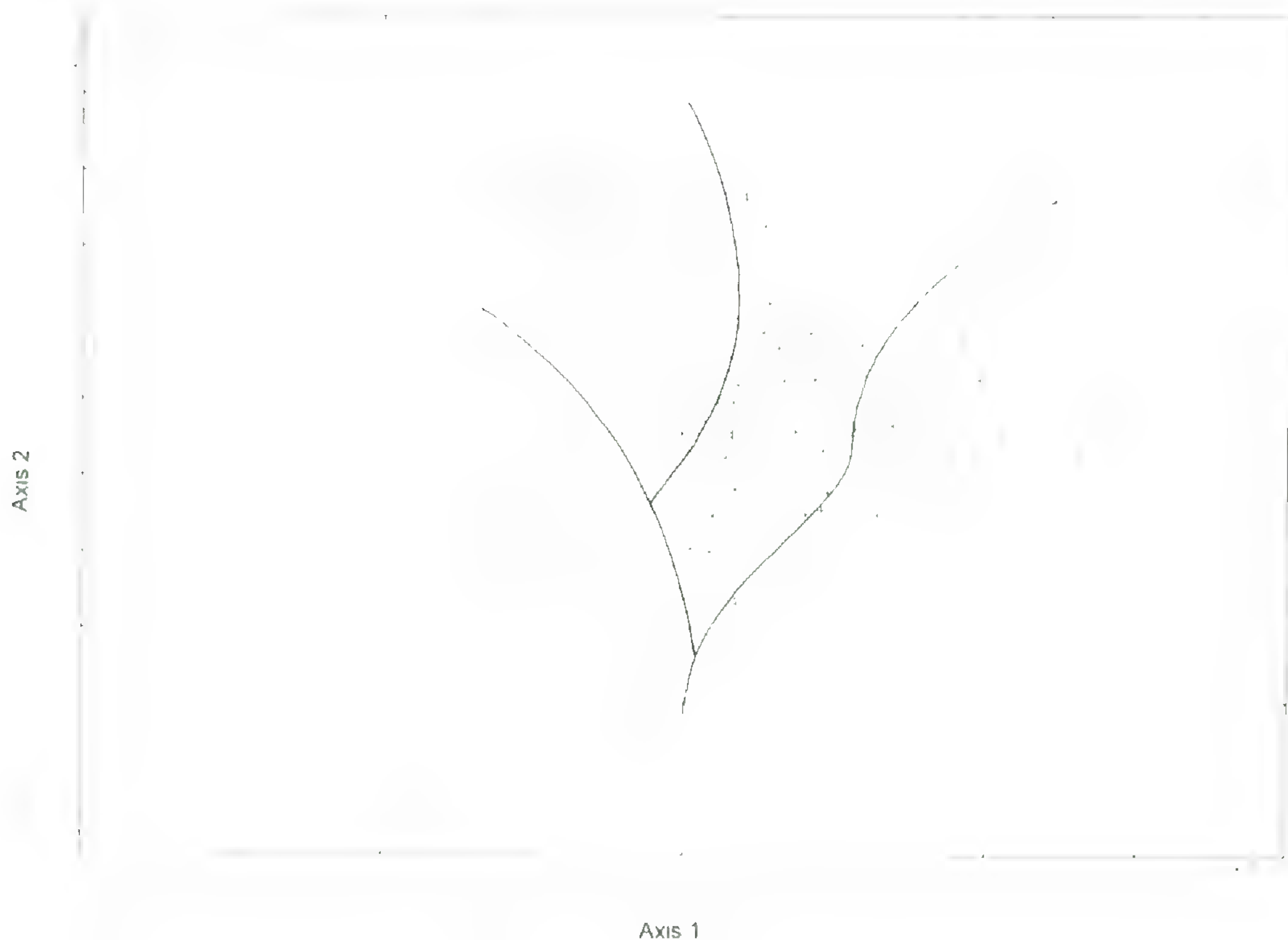


Figure 3. Plot of detrended correspondence analysis sample ordination, Axes 1 and 2, for transects in 15 beaver-impacted wetlands based on modified importance values ≥ 5 after removing Zone 1 transects. Solid lines indicate that the four community types identified by TWINSpan are ordinated by CANOCO into contiguous groups with relatively few outliers. Axis 1 represents a moisture gradient, with wettest transects on the left, driest transects on the right. Numbers indicate four community types identified by TWINSpan: 2 – *Leersia oryzoides*–*Lysimachia terrestris* Community, 3 – *Calamagrostis canadensis*–*Carex stricta* Community, 4 – *Typha latifolia*–*Eupatorium perfoliatum* Community, 5 – *Dulichium arundinaceum*–*Ilex verticillata* Community.

Of the 147 species sampled in Zone 3, emergent hydrophyte was the most common life form. Tussock-forming or tussock-colonizing graminoids predominated in many wet meadows, sometimes forming nearly pure stands. A tussock forms when dead culms and leaves persist at the plant base. With each new season the plant grows higher, sometimes forming a pillar 0.5 m or more above the wet substrate. Three graminoids associated with tussocks in this study included *Carex stricta*, *Calamagrostis canadensis*, and *Phalaris arundinacea*. It is likely that *C. stricta* was responsible for formation of most tussocks which were later colonized by *C. canadensis* and *P. arundinacea*, sometimes to the exclusion of *C. stricta*. Other taxa that frequently invaded

Table 7. Characteristic taxa for the five physiographic zones as identified by TWINSpan. Included are taxa with high MIVs in each zone and low MIVs in the other zones. Taxa with high MIVs in more than one zone are not included.

Taxa for Zones 1, 2, and 3	Taxa for Zones 4 and 5
ZONE 1 <i>Lemna minor</i> L. <i>Najas flexilis</i> (Willd.) Rostk. & Schmidt <i>Potamogeton natans</i> L. <i>Utricularia vulgaris</i> L.	ZONE 4 <i>Aster puniceus</i> L. <i>Carex atlantica</i> L. Bailey <i>Carex comosa</i> F. Boott <i>Carex crinita</i> Lam. <i>Carex stipata</i> Muhl. <i>Eupatorium maculatum</i> L. <i>Eupatorium perfoliatum</i> L. <i>Glyceria canadensis</i> (Michx.) Trin. <i>Impatiens capensis</i> Meerb. <i>Juncus effusus</i> L. <i>Polygonum sagittatum</i> L. <i>Spiraea tomentosa</i> L. <i>Triadenum virginicum</i> (L.) Raf. <i>Typha latifolia</i> L.
ZONE 2 <i>Agrostis gigantea</i> Roth <i>Eleocharis acicularis</i> (L.) Roem. & Schult. <i>Eleocharis ovata</i> (Roth) Roem. & Schult. <i>Eleocharis palustris</i> L. <i>Euthamia graminifolia</i> (L.) Nutt. <i>Galium tinctorium</i> L. <i>Galium trifidum</i> L. <i>Leersia oryzoides</i> (L.) Sw. <i>Ludwigia palustris</i> (L.) Elliott <i>Lycopus virginicus</i> L. <i>Lysimachia terrestris</i> (L.) BSP. <i>Mentha arvensis</i> L. <i>Penthorum sedoides</i> L. <i>Scirpus atrovirens</i> Willd. <i>Scirpus cyperinus</i> (L.) Kunth <i>Solidago canadensis</i> L.	ZONE 5 <i>Acer rubrum</i> L. <i>Alnus incana</i> (L.) Moench <i>Betula alleghaniensis</i> Britton <i>Betula papyrifera</i> Marshall <i>Bidens cernua</i> L. <i>Carex vulpinoidea</i> Michx. <i>Cornus amomum</i> Mill. <i>Drosera rotundifolia</i> L. <i>Dulichium arundinaceum</i> (L.) Britton <i>Equisetum arvense</i> L. <i>Ilex verticillata</i> (L.) A. Gray <i>Myrica gale</i> L. <i>Onoclea sensibilis</i> L. <i>Osmunda regalis</i> L. <i>Prunus serotina</i> Ehrh. <i>Salix sericea</i> Marshall <i>Solidago patula</i> Muhl. <i>Sphagnum</i> spp. <i>Spiraea alba</i> DuRoi var. <i>latifolia</i> (Aiton) Dippel <i>Thelypteris palustris</i> Schott <i>Vaccinium corymbosum</i> L.
ZONE 3 <i>Calamagrostis canadensis</i> (Michx.) P. Beauv. <i>Carex intumescens</i> Rudge <i>Carex lacustris</i> Willd. <i>Carex stricta</i> Lam. <i>Hypericum ellipticum</i> Hook. <i>Phalaris arundinacea</i> L. <i>Viburnum dentatum</i> L. var. <i>lucidum</i> Aiton	

tussock crowns and/or colonized hollows included *Carex intumescens*, *Galium tinctorium*, *Impatiens capensis*, *Lysimachia terrestris*, and *Triadenum virginicum*. Taxa sometimes occurring in Zone 3 that may have persisted through previous occupations included *Acer rubrum*, *Alnus incana*, *Ilex verticillata*, *Salix sericea*, *Spiraea alba* var. *latifolia*, and *S. tomentosa*.

Zone 4, drier meadow: *Typha latifolia*–*Eupatorium perfoliatum* Community

Zone 4 occurred still farther upstream on moist soils seldom affected by water level fluctuations.

Of the 155 species recorded in Zone 4, the major life forms were emergent hydrophyte, shrub, and tree seedling. The most important species was *Typha latifolia*, which often occurred in large pure stands anchored to the wetland substrate by proliferating creeping rhizomes. Common graminoids included *Carex crinita*, *Glyceria canadensis*, *Juncus effusus*, and *Leersia oryzoides*. Other herbs present were *Eupatorium maculatum*, *E. perfoliatum*, *Euthamia graminifolia*, *Impatiens capensis*, *Onoclea sensibilis*, *Polygonum sagittatum*, *Solidago canadensis*, *Thelypteris palustris*, and *Triadenum virginicum*. *Alnus incana* and *Spiraea alba* var. *latifolia* were the most important shrubs.

Zone 5, dry meadow/upland margin: *Dulichium arundinaceum*–*Ilex verticillata* Community

Zone 5 occurred farther upstream, usually on drier, seldom re-flooded soils in a narrow band along the wetland/upland ecotone. In most sites this zone was sampled only by one or two quadrats at the ends of transects through Zones 3 and 4. In only three sites were transects placed exclusively through Zone 5: Conway 1, Conway 2, and Conway 4. Because of their location close to the watershed boundary and with little topographic gradient, these three sites exhibited an unusual combination of high water table and large percent cover of shrubs and trees.

Of the 128 species found in Zone 5, emergent hydrophyte, shrub, and tree sapling were the most common life forms. *Dulichium arundinaceum* was the most important taxon in this zone (mostly due to its high MIV in Conway 2) followed by *Spiraea alba* var. *latifolia*, *Ilex verticillata*, and *Alnus incana*. Woody taxa more typical of the surrounding upland including *Acer rubrum*,

Betula alleghaniensis, *B. papyrifera*, *B. populifolia* Marshall, and *Prunus serotina* Ehrh. could also be found in this zone, though in low densities. A diverse herbaceous stratum grew under this canopy including *Carex comosa*, *C. atlantica*, *C. stricta*, *Galium tinctorium*, *Onoclea sensibilis*, *Osmunda regalis*, and *Scirpus cyperinus*. Species of *Sphagnum* were abundant, often forming a nearly continuous mat on the substrate beneath the herb and shrub canopy.

All the study sites included three or more zones; four sites included all five zones. In some sites, zones were arranged in sequence along the hydrological gradient. Frequently, zone arrangement was more complex, with a lateral progression of zones parallel to the stream channel or with isolated patches of Zones 4 and 5 occurring within Zones 1, 2, and 3, especially where shrubs, typically *Viburnum* spp., *Salix* spp., or *Spiraea* spp., had survived inundation. Detailed maps of the vegetation zones of each site are presented in McMaster (1997).

Figure 4 is a bi-plot of the results of canonical correspondence analysis showing the direction and strength of the environmental variables. Numbers correspond to the five major plant communities identified by TWINSpan. Transects separated out most clearly along the gradients of site age, depth of organic matter, pH (field), and alkalinity, suggesting that these factors were most closely related to the distribution of plant communities. Mean distance to water table, pH (lab), conductivity, and dissolved oxygen concentration gradients did not appear to relate closely to plant community distributions.

Succession. Arrows in Figure 5 indicate the successional development of vegetation in a transect over time; the tail of each arrow indicates the location of the initial sampling, the head of the arrow the position of the final sampling. Arrow length is a measure of change in species composition of a site between two samplings. As no site was occupied when first sampled, all developmental sequences originate in Zones 2 or 3.

Three successional pathways are suggested by Figure 5 and depicted schematically in Figure 6. In the first pathway (Figure 5, solid arrows), the *Najas flexilis*–*Utricularia vulgaris* Community invades sites that have been flooded for at least one year. After abandonment, the sites begin to drain and the *Leersia ory-*

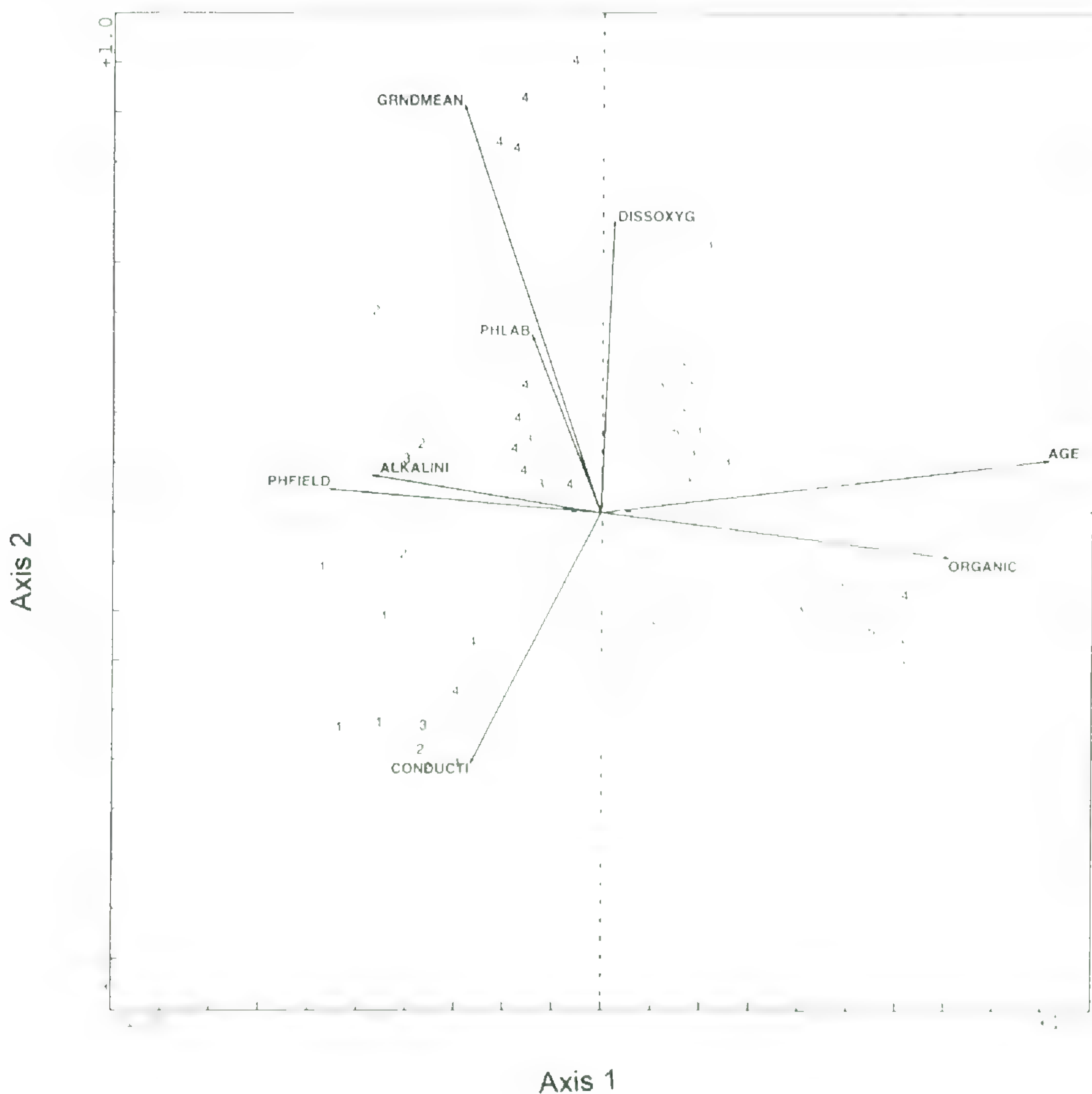


Figure 4. Bi-plot of canonical correspondence analysis sample ordination, Axes 1 and 2, for 48 transects with eight environmental variables. Arrows indicate the direction and strength of each environmental variable. GRNDMEAN = Depth of water table; DISSOXYG = Dissolved oxygen concentration; PHFIELD = pH (field); PHLAB = pH (lab); ALKALINI = Alkalinity; ORGANIC = Depth of organic matter; CONDUCTI = Conductivity; AGE = Site age. Numbers indicate five community types as identified by TWINSPAN: 1 – *Najas flexilis*–*Utricularia vulgaris* Community, 2 – *Leersia oryzoides*–*Lysimachia terrestris* Community, 3 – *Calamagrostis canadensis*–*Carex stricta* Community, 4 – *Typha latifolia*–*Eupatorium perfoliatum* Community, 5 – *Dulichium arundinaceum*–*Ilex verticillata* Community.

zoides–*Lysimachia terrestris* Community invades newly-exposed pond bottom. As draining continues, the *L. oryzoides*–*L. terrestris* Community is rapidly replaced by the *Typha latifolia*–*Eupatorium perfoliatum* Community. Within 10 to 15 years the *Dulichium arundinaceum*–*Ilex verticillata* Community is evident. In some sites, large pure stands of *T. latifolia* achieve dominance. Suc-

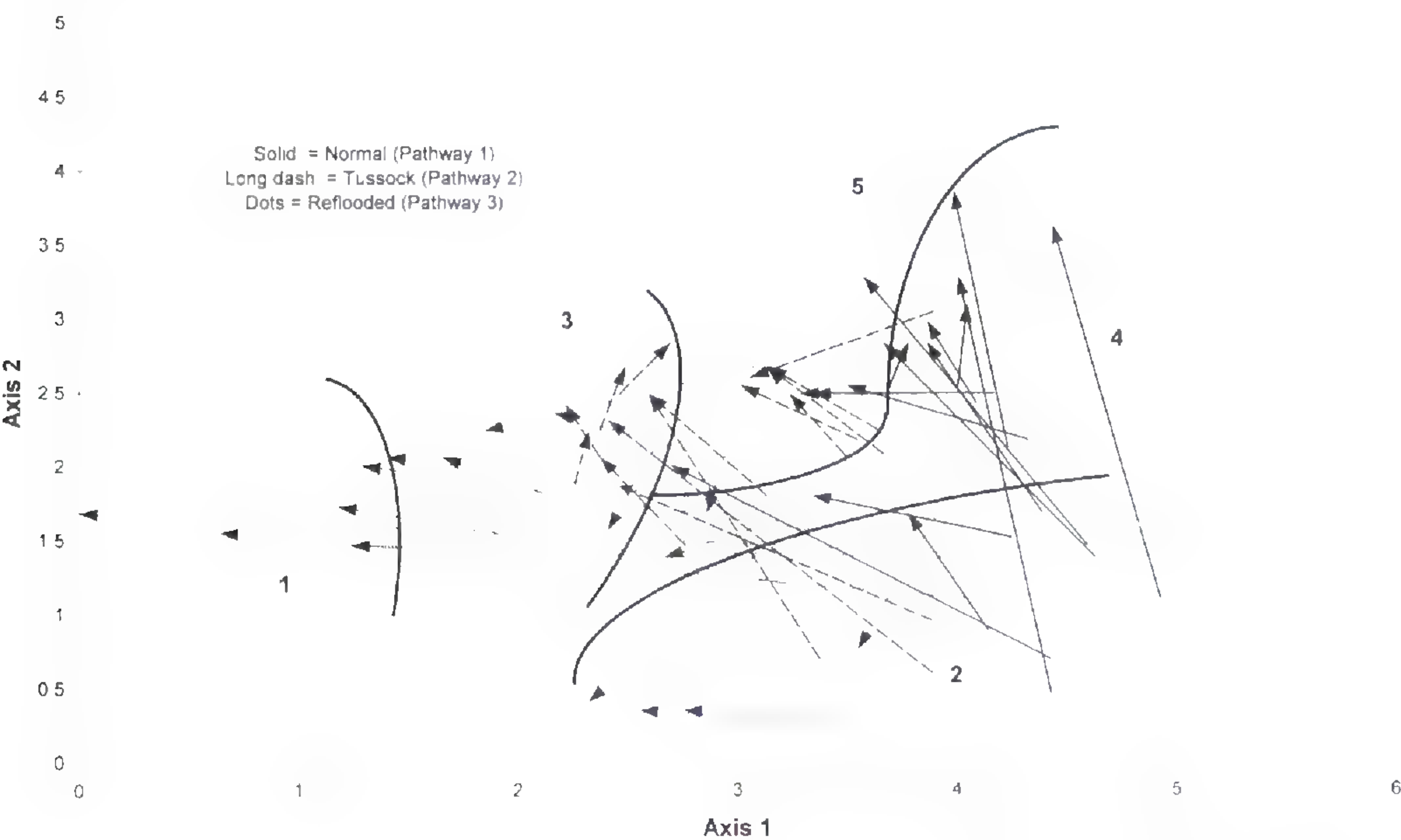


Figure 5. Plot of detrended correspondence analysis sample ordination, Axes 1 and 2, for transects in 15 beaver-impacted wetlands based on modified importance values ≥ 5 . Lines connect positions of transects sampled over 10 and 15-year intervals. Arrowheads indicate the most recent sampling. Axis 1 represents a moisture gradient, with wettest transects on the left, driest transects on the right. Numbers refer to five community types identified by TWINSpan: 1 – *Najas flexilis*–*Utricularia vulgaris* Community, 2 – *Leersia oryzoides*–*Lysimachia terrestris* Community, 3 – *Calamagrostis canadensis*–*Carex stricta* Community, 4 – *Typha latifolia*–*Eupatorium perfoliatum* Community, 5 – *Dulichium arundinaceum*–*Ilex verticillata* Community.

cession at this point often appears to be slowed or halted. Should a site remain undisturbed for more than 15 years and the soils continue to drain, succession along Pathway 1 may continue, eventually leading to development of forested wetland or upland forest. This pathway was observed in three sites: Conway 3, Conway 4, and Williamsburg 2.

A second pathway (Figure 5, dashed arrows) begins as in Pathway 1 with the *Najas flexilis*–*Utricularia vulgaris* Community succeeded by the *Leersia oryzoides*–*Lysimachia terrestris* Community. However, as the sites drain following this course of development, the *L. oryzoides*–*L. terrestris* Community is replaced within five to ten years by the *Calamagrostis canadensis*–*Carex stricta* Community. Succession may be slowed or may cease for 10–15 years or more in some sites. Sites in which this pathway was observed include Ashfield 1, Ashfield 2, Williamsburg 1, and a portion of Conway 3. The four shortest dashed arrows represent

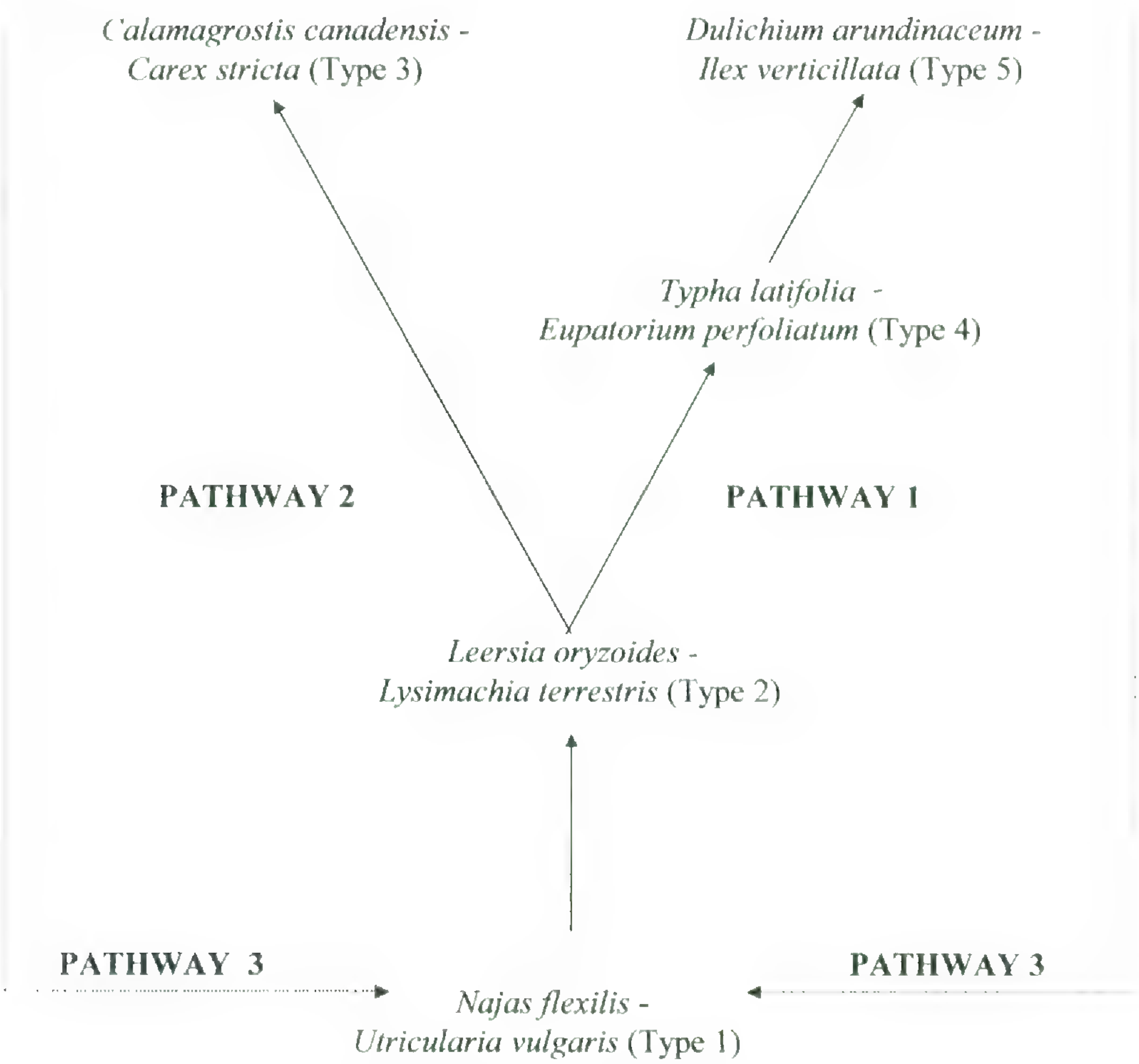


Figure 6. Schematic representation of successional pathways observed in beaver-impacted wetlands.

transects in Conway 2 where the rate of succession was slow and where small, simultaneous increases in MIV of species associated with the *C. canadensis*–*C. stricta* Community and the *Dulichium arundinaceum*–*Ilex verticillata* Community were observed.

When sites dominated by the *Leersia oryzoides*–*Lysimachia terrestris* Community or the *Calamagrostis canadensis*–*Carex stricta* Community are inundated following reoccupation, they follow a third, retrogressive pathway (Figure 5, dotted arrows), with reinvasion by the *Najas flexilis*–*Utricularia vulgaris* Community if standing water covers much of the site, or by the *L. oryzoides*–*L. terrestris* Community if exposed mud flats predominate. Tussock-colonizing species and some water-tolerant shrubs survive from the earlier communities. This pathway was observed in four sites: Ashfield 3, Ashfield 4, Ashfield 5, and in a portion of Conway 3.

Acer rubrum, while present in all 15 study sites, did not occur in large quantities upon initial sampling in any site (Mean Percent Cover = 1.3 ± 0.2 for all sampled transects; range 0.1 to 8.1%). In only one site, Williamsburg 1, was there a sizable increase in percent cover of *A. rubrum* between samplings (0.7% in 1984 to 12.2% in 1994). In four sites there was a small increase ($< 3.0\%$), while in six other sites a substantial decline was observed (McMaster 1989; McMaster 1997).

DISCUSSION

While the TWINSpan classification suggests the importance of water table depth in the study sites, canonical correspondence analysis reveals only a weak correlation between depth to water table and plant community composition. Our observations of the study sites over 15 years suggest that composition and structure of vegetation in beaver-impacted wetlands are strongly influenced not simply by water table depth but by a complex of hydrological factors including frequency, extent, and duration of reflooding. Reflooding regime appears to be a function of at least three major factors in beaver-impacted wetlands: topographic gradient, size of the watershed upstream from a site, and condition of the abandoned beaver dam.

Sites with low topographic gradient, a large watershed, and/or an intact beaver dam normally drain slowly after abandonment and reflood frequently during spring runoff and following major precipitation events. These sites generally revegetate slowly and favor species tolerant of hydric soils. Because conditions are relatively uniform throughout, zonation is not pronounced in these sites. Tussock-forming and tussock-colonizing species appear to enjoy an advantage in frequently reflooded sites because the microhabitat is elevated above high water level.

Sites with high topographic gradient and a small watershed but lacking an intact beaver dam normally drain more rapidly and are less likely to be subject to seasonal reflooding. These sites generally revegetate quickly and are readily invaded by species typical of drier upland habitat. Zonation is often better developed in these sites and tussock-colonizing species are less common than in sites that are frequently reflooded. High gradient sites are often created when beaver colonies are removed, dams excavated,

and streams channelized in response to the threat of flooding to roads, railroad tracks, or agricultural fields.

Tussock-forming graminoids create a highly irregular surface with tussock crowns often 0.5 m or more above the intervening hollows. In such a complex microtopography, a single measurement of depth to water table may bear little relationship to the hydrological conditions experienced by all members of the plant community. In a study of six peatlands in Alberta, Canada, Karlin and Bliss (1984) observed pronounced differences, not only in soil moisture but also in substrate chemistry, that were found to influence differences in plant community composition between tussock crowns and hollows.

Species composition of recently abandoned beaver wetlands in this study is clearly related to depth to water table. As sites age, however, the relationship between water table and composition becomes less clear. Succession in some draining beaver ponds appears to follow the classical hydrarch successional sequence from submersed or floating-leaved hydrophytes to emergents to small shrubs and trees (Pathway 1). The invasion of tussock-colonizing species (Pathway 2), however, appears to alter the course of succession in some sites. While the tussock and hollow microtopography might be expected to provide niches for a greater diversity of species and opportunities for more rapid successional development, in our study sites diversity declined and succession appeared to slow or stop following tussock formation, probably a result of intense root competition within tussocks and the influence of anoxic soils and deep shade in hollows.

The appearance of some woody species along the upland margins of old, well-drained sites was likely a result of recruitment from the surrounding upland forest. However, the occurrence of certain shrubs, especially species of *Spiraea*, *Alnus*, and *Viburnum*, immediately above the dam in sites of all ages suggests that many had survived inundation and continued to grow in the abandoned site. Similarly, tussock-colonizing graminoids appeared to be well-suited to fluctuating water tables and able to survive repeated occupations and abandonments. Some aspects of the composition of a site may thus be more or less indifferent to the current conditions, and may exist because of conditions that persisted or events that occurred years or even decades in the past.

Forested wetlands, especially those dominated by *Acer rubrum*, are a common feature of the landscape in the glaciated north-

eastern United States, covering 8 to 16% of some counties in eastern Massachusetts. West of the Connecticut River in Massachusetts, on the other hand, forested wetlands are uncommon, covering less than 3% of the land surface, probably due to greater topographic relief and the distinctive surficial geology and runoff patterns of that region (Golet et al. 1993). Could long-abandoned beaver wetlands in the study area follow a developmental pathway to forested wetland rather than to upland forest as described above? In only one of our sites, Williamsburg 1, was a major trend toward forested wetland observed over the duration of this study. Soil moisture and nutrient availability, both of which result from topographic gradient, may be predictors of long-term changes in the woody composition of the study sites. Where topographic gradient is greatest, even an intact abandoned beaver dam may not affect the water table enough to keep upland species from invading. Where topographic gradient is low, the water table may remain sufficiently high and nutrients in limited supply, even in the absence of beavers or their dams, so as to prevent the growth of *Acer rubrum* beyond the seedling stage (Golet et al. 1993; Moizuk and Livingston 1966). Sedge tussocks, by providing a raised substrate, have been observed to facilitate establishment and growth of *Acer rubrum* seedlings (Golet et al. 1993), a phenomenon observed in Williamsburg 1, but in other sites in this study tussocks more often excluded woody species rather than promoted them. The two sites with greatest percent cover of *A. rubrum* in 1995 were also among the most acidic, suggesting that low pH, which tends to inhibit nutrient uptake, may play a role in regulating growth of trees in long-abandoned sites.

Wetland seed banks usually include species of local provenance (Smith and Kadlec 1983; ter Heerdt and Drost 1994; van der Valk and Davis 1978). In this study several woody species present in the adjacent upland were represented in the wetland, notably *Acer rubrum*, *Betula populifolia*, *Picea abies*, and *Pinus strobus*, although few individual seedlings or saplings fell within sampled quadrats. Upland species occurred in three sites that have followed Pathway 1 for 20 years or more. Further study will be required to determine whether and to what degree the adjacent upland vegetation influences later successional stages in the study sites.

Among the water chemistry parameters examined in this study, pH (field) and alkalinity proved to be most strongly associated

with plant composition. In the four oldest, most acidic sites (Group IV), pH (field) and alkalinity decline, possibly as a result of the presence of organic acids within the accumulating sediments, which may be a result of the metabolic activity of *Sphagnum* spp. itself. In younger sites water chemistry appears to be less important than reflooding regime in influencing composition and structure of vegetation.

The beaver-impacted wetlands in this study were spatially and temporally complex. Site physiography was influenced by geological factors such as basin morphology, outcrops of bedrock, and glacial erratics; by beaver artifacts such as dams, lodges, and food caches; and by human artifacts such as walls, road fills, and excavations. All these factors affect moisture gradient, which in turn influences vegetational composition and structure. Furthermore, some members of the wetland plant community, including several shrubs and tussock-colonizing graminoids, play a significant role in altering site physiography as they create their own elevated soils and thus are buffered against fluctuating water levels. Finally, the repeated occupation and abandonment of sites by beavers, their foraging and dam-building, and periodic human disturbances such as trapping, filling, and draining, make these wetlands dynamic, ever-changing systems.

ACKNOWLEDGMENTS. I am indebted to C. John Burk, dissertation advisor to both authors, and to committee members Margaret E. B. Bigelow, Allen H. Curran, Paul J. Godfrey, David L. Mulcahy, William A. Patterson III, Karen B. Searcy, and Stephen G. Tilley. I also thank Robert M. Newton for his assistance with water chemistry analysis and Jessie Gunnard, Tasha Rimany, and Louise Mead for assistance in the field. Financial support was provided by the Department of Biological Sciences at Smith College, the Biology Department at the University of Massachusetts, Amherst, the Sigma Xi Scientific Research Society, the B. Elizabeth Horner Research Fellowship at Smith College, the Connecticut River Watershed Council, and the Massachusetts Natural Heritage Program. This paper is dedicated to the memory of Nancy D. McMaster.

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NEW ENGLAND NOTE

A NEW MASSACHUSETTS RECORD FOR *ORNITHOPUS SATIVUS* (FABACEAE)

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Ornithopus sativus Brot. Massachusetts: Nantucket Co., Nantucket, 41°17.52'N, 69°59.70'W, in sandy disturbed area ca. 200 ft. W of Polpis Rd. 0.65 mi. S of intersection with Quidnet Rd., small population with *Panicum* spp., *Desmodium ciliare*, and *Rubus* spp. on sandy slope N and W of constructed wetland, 29 Aug 2000, Standley s.n. (NEBC).

A small population of the introduced European legume *Ornithopus sativus* subsp. *sativus* was found in a disturbed sandy area on Nantucket. The taxon is reported to occur in Suffolk Co., New York (Gleason and Cronquist 1991; Magee and Ahles 1999; Mitchell 1986), but has not previously been recorded in Massachusetts (Sorrie and Dunwiddie 1996; Sorrie and Somers 1999), Rhode Island (Gould et al. 1998), Maine (Campbell et al. 1995), or the southeastern United States (Isley 1990). No specimens were found in the University of Massachusetts (Amherst) or New England Botanical Club herbaria (K. Searcy and R. Angelo, pers. comm.).

The plants were growing in an area recently disturbed for construction of a compensatory wetland, and were discovered during annual monitoring of the mitigation area. It is likely that the species occurs elsewhere on the island, as sand used in the construction of the site was obtained from other locations on Nantucket, but was not imported from any off-island source. *Ornithopus sativus* is an annual native to dry sandy areas, and is cultivated as a fodder crop (Ball 1968). It is likely to persist on Nantucket since suitable habitats are abundant, but is unlikely to become a problem invasive due to its annual habit and small size.

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NEW ENGLAND NOTE

A NEW RECORD FOR *ALLIARIA PETIOLATA*
(BRASSICACEAE)
IN HILLSBOROUGH COUNTY, NEW HAMPSHIRE

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Garlic mustard [*Alliaria petiolata* (M. Bieb.) Cavara & Grande, Brassicaceae] is a European native, first recorded in North America in 1868, and in New England in the 1890s (Nuzzo 1993a). The species is a biennial in North America, though a “winter annual” in Europe, and is adapted to a wide range of conditions (Anderson et al. 1996; Cavers et al. 1979). In some areas of North America it is displacing native vegetation (Cavers et al. 1979; Nuzzo 1993b; White et al. 1993). This article establishes its presence in Hillsborough County and notes other reports of its presence in New Hampshire and adjacent counties in Massachusetts.

Current handbooks on the New England flora have not yet caught up with the spread of this species. Gleason and Cronquist (1991) describe it as being found “throughout our range,” though it has not been reported for New Hampshire in other regional floras (Magee and Ahles 1999; Seymour 1993). Herbarium specimens and other reports, however, establish it firmly in New Hampshire at least since 1989. It has been reported from Sullivan County at two Cornish sites (Anderson 1997; Angelo 1989) and in Plainfield at the Plainfield Sanctuary of the New England Wildflower Society (Mattrick 2000). It has also been collected in Westmoreland in Cheshire County (*Boufford, Brackley & Dutton* 27,087 NEBC) and in Durham in Strafford County (*DeWees* 27 NHA). *Alliaria* has been collected in all adjacent counties in Massachusetts (Hunt et al. 1995; Magee and Ahles 1999).

In beginning a floristic survey of the Hillsborough County area, I have encountered two stations of garlic mustard in the Wilton-Lyndeborough area in south-central New Hampshire. At the first station a flowering individual was noted on May 13, 2000 on a lawn in Lyndeborough, near the intersection of Old Temple and Pettingill Hill Roads. A photograph was taken as a voucher

(*Drayton s.n.* NHA 88,425). No seedlings (first year rosettes) or other flowering individuals were observed, suggesting that this station represents an initial colonization event of one or a few seeds in the years immediately preceding (Drayton 1999). A second flowering plant was noted in Wilton on May 15, 1999 along the Burton Highway, approximately 200 m west of its intersection with the Isaac Frye Highway. No seedlings were noted. This population was not vouchered.

Alliaria petiolata has no known dispersal vector (Cavers et al. 1979). Passive dispersal is a common characteristic of herbs in deciduous forests and forest margins where this species is largely found (Drayton 1999; Hughes and Fahey 1988). The seeds fall to the ground upon the dehiscence of the siliques, and most of the seeds fall no further away than the height of the mother plant. Studies of the distribution of *Alliaria* suggest that some secondary dispersal occurs by tracking of fallen seeds by human and animal feet and vehicle tires, and occasionally by surface water run-off and similar agents.

New colonies of *Alliaria petiolata* can be quite inconspicuous, especially in the edge habitat along roads and similar corridors where the species is spreading. Thus, substantial populations can be established, creating “nascent foci” (Moody and Mack 1988) that are very difficult to exterminate. The reports from southern New Hampshire suggest that this process is well under way. Early detection and eradication is the best way to prevent explosive growth (Drayton and Primack 1999; Nuzzo 1996).

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NOTE

NYMPHAEA (NYMPHAEACEAE) IN BOLIVIA:
NOTES ON SEVERAL SPECIES, THREE NEW COUNTRY
RECORDS, AND A KEY TO SPECIES

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The most comprehensive floristic account for Bolivia is the checklist published by Foster (1958), however, no species of *Nymphaea* were included. Yet Wiersema's (1987) monograph of *Nymphaea* subgen. *Hydrocallis* included three species of *Nymphaea* as occurring in Bolivia: *N. amazonum* Mart. & Zucc., *N. gardneriana* Planchon, and *N. belophylla* Trickett (one locality). A fourth species, *N. glandulifera* Rodschied, was recorded by Haase and Beck (1989) from a single locality in an inundated savanna in northern Bolivia.

As part of an investigation of the biodiversity of aquatic plants in Bolivia, we have encountered three species of *Nymphaea* previously unknown for the country: *N. oxypetala* Planchon, *N. lingulata* Wiersema, and *N. jamesoniana* Planchon. Two additional species encountered, *N. belophylla* and *N. glandulifera*, previously known for Bolivia from single records, are briefly discussed. A key to all known Bolivian species is provided with the addition of *N. prolifera* Wiersema, an easily overlooked species anticipated as occurring in drier areas in southeastern Bolivia and already known from adjacent Paraguay. To date, all species occurring in Bolivia belong to subgenus *Hydrocallis* and are night-blooming.

SPECIES NOTES

***Nymphaea belophylla* Trickett.** *Nymphaea belophylla*, an extremely poorly known species, was thought to be restricted to the central regions of the Amazon and Orinoco basins (Wiersema

1987). The type locality is the Río Guaporé (also known as the Río Iténez) which forms the Brazil-Bolivian border, however the type material appears to be lost (Wiersema 1987). The new report of *N. belophylla* is from Laguna Cáceres in the Bolivian Pantanal on the border with Brazil. The discovery was not wholly unexpected as the species was recently listed for a nearby area of the Brazilian Pantanal by Pott and Pott (1997).

Nymphaea belophylla was encountered in an extensive, seasonally flooded plain adjacent to the channel of Río Sicurí, a few kilometers upstream from Laguna Cáceres. This area was contiguous with the lake during the rainy season and had a water depth of ca. 1.5–2 m at the time of the visit. The area was dominated by *Oryza rufipogon* Griffith and *Paspalum wrightii* Hitchc. & Chase. *Nymphaea belophylla* was scattered and occasional. The flowers, cut open, had a sweet, fruity scent; no fruits were observed.

VOUCHER SPECIMEN. BOLIVIA. Dept. Santa Cruz: Prov. German Busch, Río Sicurí, a few km above where it empties into Laguna Cáceres, elev. ca. 90 m, 18°54'5"S, 57°42'19"W, 20 Jul 1998, Ritter, Crow, Garvizu & Crow 4655 (MO, NHA, USZ).

***Nymphaea glandulifera* Rodschied.** *Nymphaea glandulifera* is widely distributed in Central and South America (Wiersema 1987). Although this species was not listed for Bolivia in Wiersema's (1987) monograph, it had since been reported for the Llanos de Moxos, an extensive complex of seasonally inundated savannas in Central Bolivia (Haase and Beck 1989). Our report of a population of *N. glandulifera* at Mariposa represents the southernmost extension of its range. The site was a small pool occupying a wide section of a (seasonal?) stream. The plants were locally abundant and flowers were present.

VOUCHER SPECIMEN. BOLIVIA. Dept. Cochabamba: Prov. Carrasco, Mariposa, wetland on the northern side of the highway to Santa Cruz, ca. 1.5 km E of town, elev. 220 m, 17°00'39"S, 65°02'03"W, 5 Mar 1995, Ritter 1642 (BOLV, MO, NHA).

***Nymphaea jamesoniana* Planchon.** *Nymphaea jamesoniana* is widespread throughout tropical and subtropical America (Wiersema 1987), hence, the report of its presence in eastern Bolivia on the Brazilian border in Parque Nacional Noel Kempff Mercado

was not unexpected. The site, Lago Caimán, was a long, fish-hook-shaped “bahía” (a lacustrine system which is connected with a nearby river during high water stages) associated with the nearby Río Iténez. *Nymphaea jamesoniana* was common, growing at depths of 1–2 m, and although the population was in flower at the time, we were able to collect only sterile material.

VOUCHER SPECIMEN. BOLIVIA. Dept. Santa Cruz: Prov. Velasco. Lago Caimán, elev. 200 m, 13°36'30"S, 60°55'36"W, 18 Apr 1996, *Ritter & Garvizu 3119* (NHA, USZ).

***Nymphaea lingulata* Wiersema.** *Nymphaea lingulata* was previously known only from northeastern Brazil (Wiersema 1987). This new report for Bolivia is from Laguna Volcan, a small (ca. 3 ha) lake in the foothills (elev. 1150 m) of the Andes in south-central Bolivia. The lake was dominated by *Potamogeton illinoensis* Morong and *P. gayii* A. Benn., with an adjacent marsh dominated by *Typha domingensis* Pers. and *Cyperus papyrus* L. Wiersema (1987) reported that fruiting in *N. lingulata* was known only from a single collection in Brazil; however, fruits have now also been collected in Guyana. Although the plant was abundant at Laguna Volcan and the population produced numerous flowers, no fruits were observed.

VOUCHER SPECIMENS. BOLIVIA. Dept. Santa Cruz: Prov. Florida, Laguna Volcan, SW of Estancia Angostura above the road to Santa Cruz, elev. 1150 m, 18°08'S, 63°39'W, 4 Feb 1996, *Ritter 2291* (MO, NHA, USZ, W); Laguna Volcan, 29 Jun 1997, *Ritter, Crow & Crow 4086* (NHA, USZ).

***Nymphaea oxypetala* Planchon.** *Nymphaea oxypetala* is known from relatively few sites. Its distribution had previously been thought to be limited to Venezuela, Ecuador, and southern Brazil, with uncertain records also listed for Cuba and Paraguay (Wiersema 1987). Our Bolivian collections extend the range to two areas in eastern Bolivia: (1) the Río Paraguá in Parque Noel Kempff; and (2) two populations in the Bolivian portion of the Gran Pantanal of Mato Grosso. *Nymphaea oxypetala* is unusual for the genus in that the leaves are almost always strictly submersed, although occasionally very reduced floating leaves are also produced. This may explain why this less-than-conspicuous species is known from so few localities. The floating, night-

blooming flowers of *N. oxypetala* have very acuminate perianth parts and the longest carpellary appendages of any *Nymphaea*.

At the Río Paraguá site, the plants were growing in a portion of the river adjacent to the village of Florida where the river margins were kept free of floating vegetation by human activities. A small population was present in depths up to ca. 2 m. The petioles appeared to be rather fragile, with many leaves broken off and floating in the area.

In the Pantanal site at Puesto Gonzalo, *Nymphaea oxypetala* was found growing in openings in floating vegetation mats and in areas where human activities kept the margins free of floating mats. Although locally abundant, no fertile individuals were observed. The other Pantanal population was encountered in the same general area as *N. belophylla* (as described above).

VOUCHER SPECIMENS. BOLIVIA. Dept. Santa Cruz: Prov. Velasco, Reserva ecológica El Refugio, a 300 m al E del campamento Toledo sobre el camino hacia el Río Paraguá, Barbecho anegado temporalmente, 14°42'32.7"S, 61°09'18.9"W, elev. 200 m, 16 May 1995, *Guillén & Medina 3723* (NHA, USZ); Prov. Velasco, Río Paraguá, alongside the community of Florida, elev. ca. 200 m, 14°36'55"S, 61°11'55"W, 22 Mar 1996, *Ritter 3003* (MO, NHA, USZ); Prov. Angel Sandoval, Puesto Gonzalo, along a side channel of the Río Pando near the Bolivian-Brazilian border, elev. ca. 90 m, 17°40'12"S, 57°46'53"W, 12 Jul 1998, *Ritter, Crow, Garvizu & Crow 4491* (MO, NHA, USZ), Prov. German Busch, Río Sicurí, a few km above where it empties into Laguna Cáceres, elev. ca. 90 m, 18°54'5"S, 57°42'19"W, 20 Jul 1998, *Ritter, Crow, Garvizu & Crow 4653* (MO, NHA, USZ).

KEY TO THE SPECIES OF *NYMPHAEA* IN BOLIVIA

1. Leaf blades sagittate, over 1.8 times as long as wide ... (2)
 2. Mature leaves mainly submersed; sepals and outer petals acuminate *N. oxypetala*
 2. Mature leaves floating; sepals and outer petals rounded to acute *N. belophylla*
1. Leaf blades suborbicular to elliptic, less than 1.6 times as long as wide ... (3)
 3. Leaves with ring of pubescence at apex of petiole *N. amazonum*
 3. Leaves lacking ring of pubescence at apex of petiole ... (4)
 4. Only outer petals in tetramerous whorls, inner spirally arranged (5)

5. Carpellary appendages lingulate-tapering, petals 8–14, tuberiferous flowers lacking; leaf blades uniformly green on upper surface . . . *N. lingulata*
5. Carpellary appendages clavate, petals 19–35, tuberiferous flowers usually present; leaf blades usually with purple flecks or blotches on upper surface (although not yet found, may occur in southeastern Bolivia) *N. prolifera*
4. All petals in tetramerous whorls (6)
6. Leaf blades lacking evident cross veins centrally, or if present very faint, the venation radiate, uniformly green on upper surface
. *N. glandulifera*
6. Leaf blades with evident cross veins centrally, the venation weblike, often with colored markings on upper surface (7)
7. Plants producing stolons throughout growing season; leaf blades usually mottled with rusty brown pigment, especially below; carpellary appendages 8–20 mm long
. *N. gardneriana*
7. Plants not stoloniferous; leaf blades often with dark flecks on both surfaces; carpellary appendages 3–7 mm long *N. jamesoniana*

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NOTE

CYPERUS DIANDRUS: ANOTHER NOVA SCOTIAN RARE
PLANT FROM A RARE LAKE TYPE

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On 17 August, 2000, when the lake water level had fallen to its lowest seasonal elevation (1.97 m below winter high water level), I discovered numerous (> 500) individuals of the annual *Cyperus diandrus* Torr. at the water's edge of Third Lake, Canaan, Yarmouth Co., Nova Scotia (Hill, Hill & Hill s.n., ACAD ECS015836). The plants were diminutive (2–3 cm tall), among the smallest on record (range: 2–45 cm; Fernald 1950). Other characteristically small plants [*Ranunculus reptans* L. and *Eleocharis acicularis* (L.) Roem. & Schult.] were associated with *C. diandrus* at the waterline and all were in fruit.

Cyperus diandrus has a G5 ranking. It occurs in 26 states of the U.S.A. and is considered rare in nine (NatureServe 2000). *Cyperus diandrus* had been known to occur from Ontario to Quebec, to central Maine, south to New Mexico and South Carolina (Scoggan 1985). The closest known populations to this Nova Scotian site are in New Brunswick. Early findings in New Brunswick by Fowler and Macoun (Scoggan 1985) were substantiated and the taxon is listed in *The Rare Vascular Plants of New Brunswick* as occurring at two locations (Hinds 1983). A 1998 listing for the taxon in Nova Scotia (Haines and Vining 1998) was in error (T. F. Vining, pers. comm.) but the current finding now remedies this.

Cyperus diandrus occurs in a variety of wetland habitats from tidal flats to pond shores. Its Nova Scotian locality, the shoreline of a large catchment area lake (67,000 ha; Third Lake catchment area) is itself a rare habitat type since, of Nova Scotia's approximately 2000 lakes, only a minority have watershed areas greater than 50,000 ha. These habitats are regional "hot spots" for rare Atlantic Coastal Plain plant species (Hill et al. 1998). It has been suggested that many rare species in these habitats are poor competitors and are locally abundant because the greater flooding in

large catchment area lakes maintains the low biomass conditions they require (Wisheu and Keddy 1994). *Cyperus diandrus*, although not a coastal plain species, occurs in the most flood-stressed part of this habitat: at the lowest shoreline position that has a terrestrial phase. The growing season at this position is the shortest available on the lakeshore. Annuals are not common in this habitat (Keddy and Wisheu 1989) and populations of annuals are especially vulnerable to between-year variation in water level; a high water year could prevent an annual from successfully establishing seedlings. *Cyperus diandrus* was discovered in 2000, which followed two low-water summers; April to August precipitation totals for 1999 and 1998 were 25% and 23% lower than average (1960–1999 data, Environment Canada, Yarmouth, Nova Scotia). This annual may be able to persist in a narrow zone, bounded at upper shore positions by increased competition in a higher biomass habitat and at lower shore positions by growing seasons that do not allow for seed production. Thus, the species appears to be one of the more vulnerable in this lakeshore community. Annual changes in its population should be monitored and an investigation of its reproductive biology should be undertaken. As a first step, it needs to be determined whether the species has formed a persistent seed bank that can sustain the population during periods of high water level (cf. Keddy and Reznicek 1982).

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BOOK REVIEW

Flora of Florida by Richard P. Wunderlin and Bruce F. Hansen. 2000. *Volume 1. Pteridophytes and Gymnosperms*, xii + 365 pp. illus. ISBN 0-8130-1805-6 \$49.95 (hardcover). University Press of Florida, Gainesville, FL.

This first volume of the *Flora of Florida* has long been in preparation, and it is a pleasure to finally see it in print. The *Flora of Florida* project formally began in the early 1980s; although started by Donovan Correll and Richard Wunderlin, it has since involved numerous individuals. In addition to the introduction, the book includes sections on the “Physical Setting” and “Vegetation of Florida” (both by R. L. Myers), “Botanical Exploration in Florida” (by R. P. Wunderlin, B. F. Hansen, and J. Beckner), the systematic treatment of “Pteridophytes” (by C. E. Nauman, R. P. Wunderlin, and B. F. Hansen, with Isoetaceae contributed by W. C. Taylor and N. T. Luebke, and spore descriptions contributed by A. F. Tryon), and the systematic treatment of “Gymnosperms” (by R. P. Wunderlin and B. F. Hansen). The flora includes numerous illustrations and photos; the systematic section is graced with 68 beautiful technical drawings, representing each of the genera included in the flora. Of these, 50 were drawn by P. Fawcett—29 original and 21 previously published figures, the latter mainly from Correll and Correll (1982). Eighteen figures are by W. Jurgens (all original illustrations).

The section on the “Physical Setting” includes information on the physiography, geology, soils, climate, and importance of fire in the state’s plant communities. The plant communities of Florida are carefully described following the system of Myers and Ewel (1990), including pine flatwoods, high pinelands, scrub, temperate hardwood forest, tropical forests, coastal strand, freshwater swamps, freshwater marshes, salt marshes, mangroves, and the aquatic vegetation of rivers and streams, lakes, and inshore marine environments. The treatment of each community includes a discussion of major variants, characteristic substrate conditions, a listing of important species, and the impact of fire on the vegetation. Both chapters include numerous useful literature citations.

The history of botanical exploration in Florida is divided into sections covering major botanical explorations and floristic work

during the following periods: Prehistory and early European contact (pre-1513), European exploration (1565–1765), Early floristic botanists (1765–1821), Torrey and Gray (1821–1901), John Kunkel Small (1901–1938), and Revisionists and monographers (1938–present). These sections are quite detailed, giving the reader a vivid summary of the activities of the major collectors and botanists who have worked in the state. Important floristic and biogeographical works also are cited. It would have been nice if the popular identification guides of G. Nelson (1994, 1996, 2000) had been cited. Although the collectors L. M. and L. F. Baltzell are mentioned, the work based upon their collections (Hall 1993) is not, but these are a mere quibbles.

Florida, with just under 4000 native and naturalized vascular plant species (Wunderlin 1998), has the third most diverse flora of any state in the United States, trailing only California and Texas. Part of this diversity reflects the state's location and shape—a long peninsula with warm temperate forest in the north grading into subtropical moist to dry forests in the south. The flora includes a mix of temperate and tropical species (the former of eastern North American and the latter mainly Caribbean floristic affinities), as well as taxa related to those of western North America (especially in the dry sandhill and scrub communities). The state's flora, therefore, is of interest to plant systematists across a wide geographic area.

The systematic treatment includes 170 native and naturalized species (in 68 genera, 28 families): 138 ferns and relatives, 16 conifers, 14 lycopodiophytes, and 2 cycads. Excluded taxa are listed, along with the reasons for their exclusion. The species are arranged following the system of Tryon and Tryon (1982) and Kramer and Green (1990). I note that some of the familial circumscriptions result in the recognition of non-monophyletic groups (e.g., Polypodiaceae *sensu stricto*, Dryopteridaceae, Dennstaedtiaceae; see Pryer et al. 1995). Delimitation of families within the Polypodiaceae *sensu lato* (a large and exceptionally diverse monophyletic group) is, unfortunately, still rather problematic, and the authors have taken a conservative approach. Families of conifers and cycads are in agreement with those used in the *Flora of North America* (Flora of North America Editorial Committee 1993). Genera and species are arranged alphabetically (by scientific name) and synonymous scientific names as well as common names are provided. The treatment of each species (or

infraspecific taxon) includes a description, habitat summary, geographical distribution, statement of endemic or exotic status, and indication of reproductive season. One species within each treated genus is fully illustrated; numerous indented dichotomous keys are provided. Recent monographs or revisions are referenced when available.

The taxonomic treatment is of very high quality. Descriptions and illustrations are accurate, as is the up-to-date geographical information, which should be used in conjunction with the *Atlas of Florida Vascular Plants* (Wunderlin et al. 2001). The keys are carefully constructed, and worked for the specimens that I chose to try identifying with them.

It is informative to compare the treatment to that of the recently published *Flora of North America*. Seventeen differences in species names occur, representing 10% of the pteridophyte and gymnosperm flora of Florida. Some changes result from a modification of generic circumscriptions (e.g., inclusion of *Phlegmariarus* in *Huperzia*, inclusion of *Pseudolycopodiella* and *Palhinhaea* in *Lycopodiella*, and inclusion of *Cheiroglossa* in *Ophioglossum*), with the *Flora of Florida* taking, in general, a more conservative generic approach. Other changes relate to altered species circumscriptions resulting from recent taxonomic studies (e.g., plants referred to *Isoetes engelmannii*, here treated as *I. appalachiana*; the recognition of *Taxodium ascendens* as distinct from *T. distichum*; the inclusion of *Zamia integrifolia* within a broadly defined *Z. pumila*). *Juniperus virginiana* is circumscribed broadly, and varietal recognition is not given to the coastal plain populations, which were treated as var. *silicicola* in the *Flora of North America*. Finally, a few differences relate to nomenclatural matters (e.g., *Asplenium dentatum* vs. *A. trichomanes-dentatum*, *Nevrodium lanceolatum* vs. *Neurodium lanceolatum*). It is surprising that 14 species are included that were not mentioned in the *Flora of North America*; these all represent rare naturalized species, some of which have evidently become established only very recently. A few species (e.g., *Ophioglossum vulgatum*) have been documented not to occur in Florida, and these are formally deleted from the flora. These differences indicate that additional systematic work is needed, and future studies should focus on (1) determination of monophyletic groups (thus clarifying family and generic limits), (2) clarification of species limits, especially in widespread variable taxa (e.g., *Pteridium aquilinum*), and (3) in-

creasing our knowledge of distributional patterns. An especially useful aspect of the *Flora* is that the authors point out the taxonomic problems. Thus, the *Flora* is a useful guide to groups in need of additional revisionary study.

The book includes not only a "General Index" but also indices to scientific names and common names. Strangely, the heading of the index to scientific names states that "Accepted names of plants . . . are in Roman type. Synonyms and excluded species are in italics." In fact, all scientific names of genera, species, and infraspecific taxa (whether accepted or not) are in italics. However, accepted family names are in Roman type, while synonymous family names are in italics.

This is a beautiful and scientifically significant book. It will quickly become an essential reference for both students and professionals, or anyone interested in the systematics and biology of ferns or the flora of the southeastern United States. The book is reasonably priced as well. It has been worth the long wait. With the publication of this first volume, the *Flora of Florida* project has really gotten off to a great start. I am looking forward to equally fine taxonomic treatments of the dicot families (volumes 2 to 6) and the monocot families (volumes 7 and 8), which will employ a family-level classification slightly modified from the Angiosperm Phylogeny Group (1998).

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- , B. F. HANSEN, AND E. L. BRIDGES. 2001. Atlas of Florida vascular plants. Univ. of Florida Web Site (<http://www.plantatlas.ufl.edu>).
- WALTER S. JUDD, Department of Botany, University of Florida, 220 Bartram Hall, P.O. Box 118526, Gainesville, FL 32611-8526.

BOOK REVIEW

Fern Grower's Manual, Revised and Expanded Edition by B. J. Hoshizaki and R. C. Moran. 2001. 624 pp. illus. color photos, b/w photos, line drawings. ISBN 0-88192-495-4 \$59.95 (hardcover). Timber Press, Portland, OR.

This is a small review of a large volume (8 × 11 in.) Replete with information on the cultivation of ferns and their allies (pteridophytes). It is a rich source of material on all aspects of growing these plants. A large part of the work is devoted to descriptions of the plants, notes on the source of the name, and outlines of the native ranges of some 700 species. Specialists were consulted in order to insure accuracy. It is richly illustrated by silhouettes, photographs, and line drawings of details. Many of the included species are native to Malesia and are cold-sensitive species. Unless one is fortunate enough to live in the southern part of the United States or elsewhere in an amiable climate, a greenhouse is needed to grow most of these species.

The first hundred pages are devoted to information on the structure of ferns, their propagation, cultural needs, soil, and fertilizers. A central section of 50 color photographs of handsome garden ferns adds to the attractive illustrations. The price is modest in today's market for a book of this size. This work will be a useful reference for many years.

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NEBC MEETING NEWS

March 2001. Vice President Paul Somers introduced the evening's speaker, Dr. David Boufford. David came to his position as Assistant Director of Collections in the Harvard University Herbaria from the Missouri Botanical Garden and Washington University of St. Louis via the Carnegie Museum of Natural History in Pittsburgh. The staff at Harvard has been interested in the flora of the Far East for nearly a century and a half, and David Boufford is no exception. David took his first trip to Japan in 1977, followed by a series of trips to China beginning in 1980, while he was at Carnegie Museum. He currently serves on the editorial committees for the *Flora of China*, *Flora of Japan*, *Flora of Taiwan*, and the *Flora of Korea*. He will also serve for a few more months as the Executive Director of the *Flora of North America* project. He was invited to speak this evening about his most recent work and travels in China. His talk was entitled "Hengduan Mountains, China: Hotspot of biodiversity."

The Hengduan Mountains of southwestern China are one of the world's 25 designated "hotspots" for biodiversity. These hotspots make up less than four percent of the world's land area, but are estimated to harbor more than 40 percent of the world's species. Most of the hotspots are in the tropics, but other designated areas include the Cape Province of South Africa, the California Floristic Province, and the island of Madagascar. The Hengduan Mountain hotspot is one of the few, and the most diverse, in the north temperate zone. This corner of the Tibetan Plateau in eastern Tibet and western Sichuan province supports more than 3500 endemic species of vascular plants. The remarkable diversity of the region was first revealed by the work of Joseph Rock, George Forrest, and various Russian explorers. The area was explored further in the early 1940s by Dr. Shiu Ying Hu of Harvard, the first woman to carry out field work in China, and more recently by Chinese botanists. The geology of the area has almost certainly been a major influence on the biota of the area.

The Qing-Zang Plateau (Qinghai and Xizang in Tibet) began to rise about 45 MYA as several separate landmasses, and eventually the Indian subcontinent, plowed into the southern flank of Asia. The squeezing of the plateau to the southeast has resulted in a series of deep, parallel gorges on the eastern edge of the Himalayan range through which three of the world's great rivers,

the Yangtze, Mekong, and Salween, flow. At one point these rivers are only 70 kilometers from one another. The ridges above these rivers reach 6000 m in places, from 1500 m at the water's edge. Slightly farther to the west are also the Irrawaddy and the Yarlong Zangbo; the latter abruptly changes from an easterly flowing stream in southern Tibet to fall precipitously southward along the front edge of the Himalaya to become the Brahmaputra in India. The Hengduan region is the size of Texas but supports somewhere between 9000 and 12,000 species of vascular plants, representing approximately one-third of the flora of China. David painted a portrait of the Hengduan Mountains with a series of stunning photographs, and against that backdrop took us on a tour of the many and varied habitats of the region.

At 3500–3800 m a boreal forest of spruce, fir, pine, willow, and poplar creates the landscape. The herbaceous flora of these woods and forest edges comprises some of the 1200 orchids of China as well as genera such as *Lilium*, *Arisaema* (40 spp.), and *Aconitum* (100 spp.). *Primula*, *Caltha*, and *Iris* grow in associated wet meadows. The recently discovered *Acanthochlamys bracteata* is rare in dry valleys in this area. Its classification has been puzzling, having first been described in the Amaryllidaceae, then put in the Velloziaceae, and more recently placed in its own family, the Acanthochlamydaceae. Molecular evidence indicates a relationship with Velloziaceae, a family primarily of the southern hemisphere. If this placement is correct, *Acanthochlamys*, or an ancestor, may have been a passenger on the Indian raft as it traveled from the southern hemisphere to its present position. In grazed meadows at slightly higher elevation grow many plants that are distasteful or poisonous to cattle, such as *Stellera chamaejasme* (Thymelaeaceae) and *Podophyllum hexandrum* (Berberidaceae). At around 4000–4200 m alpine meadows support a rich herbaceous flora, including a yellow *Cyananthus* (Campanulaceae) and numerous composites such as *Saussurea* (more than 100 spp.), *Leontopodium* (about 25 spp.), and *Anaphalis* (28 spp.). Also found in these high meadows are more than 100 species of gentians—one-third of all of China's gentians.

At the chilly heights of 4000 m and more, *Rheum alexandrae* (Polygonaceae) creates greenhouse-like temperatures for warming insects amongst the yellow bracts of its inflorescence. If the bracts are removed, pollen does not develop normally. The inflated bracts of several species of *Saussurea*, the calyx of *Przewalskia*

(Solanaceae), and the petals of species of *Lilium* clearly offer the same advantage to developing flowers. David continued the trek through the saddles between mountains and on to the mountain crests at 4600 m. No woody vegetation can stand on the windward slopes, though *Rhododendron* thrives to leeward. The diversity of *Rhododendron* in these mountains is phenomenal: 224 species can be found in these mountains, compared with 24 for all of North America, and 32 for Nepal. Significant hybridization has occurred within the group. Yellow-flowered species can be found in large numbers. Across slopes of shale that are hot in summer, cold in winter, and constantly moving, are found very hairy species of *Phyllophyton*, *Eriophyton*, and *Saussurea* and plants with pale, light-reflective, glabrous leaves, such as in *Corydalis benecincta*. Up on the plateau itself buttercups grow at the edges of wet areas and lakes. These lakes trend from freshwater in the southeast to salty and alkaline in the desert-like interior of the plateau. Many are surrounded by thousands of yellow- or purple-flowered individuals of *Pedicularis*. Images of *Pedicularis* (215 spp. in the Hengduan area) and *Euphrasia* rounded out this most memorable presentation of one of the world's most important botanical regions.

—DON HUDSON, Recording Secretary.

April 2001. The Distinguished Speaker for 2001 was Dr. Robert Kral, Professor Emeritus of Biology at Vanderbilt University and Resident Research Associate, Botanical Research Institute of Texas. He spoke on “Biology and Management of Rare Plants in the Southeastern United States.” He began his talk with the statement “Let’s face it; you’re doomed.” However, what followed was an opportunity to hear how he became involved in an extensive project on rare plants, what constitutes a rare plant in his view, and details of a few of the over 300 rare plants discussed in his resulting book.

Dr. Kral pointed out that the original Endangered Species Act of 1973 did not include plants. He and other taxonomists were asked to develop a list of plants that was published in 1974 by the Smithsonian Institution. Shortly thereafter, Dr. Nathan Byrd of the U.S. Fish and Wildlife Service asked if he would be interested in evaluating the forest-related rare plant species in the South, an area extending from Virginia to Lake Okeechobee,

Florida, and west to Arkansas, eastern Oklahoma, and eastern Texas. Dr. Kral, who attributes his invitation to become involved to a degree in forest management, started the project in 1975. He began by developing a list of species, checking nomenclature, doing literature searches, and checking collections. He was charged with finding the rare species, developing a list of associated species, describing the habitat in such a way that it would fit into a system of forest types, discussing the impact of forestry management practices on the plants, and making management recommendations. The study, which covered some 322 taxa, was completed in 1983 with the publication of the two-volume *Report on Some Rare, Threatened or Endangered Forest-Related Vascular Plants of the South*. Editing such a work was described as a humbling experience.

An important aspect of Kral's work was to come up with management recommendations, and to do that, it was important to determine why plants were rare. Some species are rare because they have very narrowly defined niches and small population sizes, either because they are initial endemics ("baby species") or are "old species," described as "too much junk in the nucleus." In contrast, some rare species of restricted or specialized habitats are abundant or may even be considered weeds where they are found. Irrespective of the population size, these species are particularly susceptible to loss of habitat. Another group of rare plants are those that were once abundant, but have had their habitat destroyed because the "land they occupy is too valuable." These include plants of prairies and wetlands. Finally, he mentioned threats from exotics. Bob pointed out that continental drift separated many species of plants, but that "Homo saps" were reuniting them. Many of these exotics have wide tolerances and disperse rapidly, so rapidly, that some of the early explorers of North America considered some exotics to be native.

From Dr. Kral's perspective, problems that remain in protecting rare species are not just those associated with instituting recovery programs. It is important for forest and landscape managers to leave the land in a better condition than when they started. In addition, it is important to train young biologists to read the landscape as a way to help preserve biodiversity. He concluded this portion of his talk with some questions. How can trained biologists provide input before management decisions are made? Who

will become involved, and who will pay? What is the role of academic institutions in these issues?

Finally, Dr. Kral illustrated a number of the points he had made with a selection of slides. Plants illustrated included *Hymenocallis coronaria* and *Sagittaria secundifolia* growing in or near rocky, swiftly flowing streams that could be affected by changes in water level and quality. Changes in water level also affect plants of sink-hole ponds such as *Rhexia salicifolia*, *Xyris longisepala*, and *Hypericum lissophloeus*. Some of the plants found around ponds of fluctuating water level, such as *Fimbristylis perpusilla*, are abundant some years but absent others. *Zephyranthes treatiae* and *Lilium iridollae* are plants of wet areas but are maintained by periodic fire that reduces competition from other plants. In contrast, woodland species such as *Silene polypetala*, *Veratrum woodii*, *Trillium pusillum* var. *ozarkanum*, and *T. texanum*, are threatened by removal of the forest canopy. *Trillium texanum* is also threatened by erosion from the conversion of nearby sand-hill forests to pine plantations. Quite a few plants that Bob illustrated were from scrub-lands and old dunes of northern Florida that are threatened by development, including *Nolina brittoniana*, *Dicerandra immaculata*, *Asimina tetramera*, and *Liatris ohlingerae*. Some of the rare plants he mentioned, such as *Carex biltmoreana* and *Eriocaulon koernickianum*, are plants of extreme habitat and limited population size. Others, like *Leavenworthia stylosa* and *Streptanthus squamiformis*, are abundant or even weedy where they occur. A few plants, like *Clematis socialis*, are known from only single sites, while others like the pitcher plants, including *Sarracenia alabamensis*, were more widespread, but are becoming rare because of habitat loss involving drainage and invasive species. Throughout his talk, Bob's love for the region and its landscape became clear as he spoke of "Gardens of Eden" and blackwater streams that make you want to say "thank you."

—KAREN SEARCY, Recording Secretary *pro tempore*.

May 2001. Vice President Paul Somers introduced Dr. Carl W. Grobe of Westfield State College in Westfield, Massachusetts, to speak to the club on "Seaweeds: The Underappreciated model systems." Carl grew up in coastal Maine where his interest in the intertidal ecosystem was nurtured. Undergraduate work at Connecticut College and later studies at the University of California

at Davis cemented his life-long passion for seaweeds. Carl's work has extended from the Darling Center in Walpole, Maine, to the ice-bound shores of Antarctica.

Dr. Grobe prepared the audience with a systematic review of the multicellular, macroscopic marine algae that we think of as seaweeds, including the reds (Rhodophyta), browns (Phaeophyta), and greens (Chlorophyta). Seaweeds provide much of the primary productivity of marine and estuarine ecosystems and provide niches and food for many marine and intertidal organisms. In addition, this group of photosynthetic organisms is playing an increasingly important role as a source of nutrients, vitamins, and raw materials for commerce. Studies of the evolutionary history of the seaweeds have provided insights into the primordial endosymbiotic relationship between photosynthetic bacteria and early phagocytic eukaryotes, which gave rise to photosynthetic eukaryotes and the higher plants. Carl reminded us as well of the specific characteristics of the Chlorophyta as source material for the ultimate emergence of plants on land. Carl thus painted the backdrop for his own studies of the physiology of the seaweeds.

Carl is particularly interested in the life of intertidal organisms, and he has chosen the seaweeds as a model system to investigate such things as the stresses induced by the cycles of immersion and emersion and desiccation and hydration, as well as the daily and seasonal fluctuations of temperature and wave action. Although seaweeds have simplified physiology, their biochemistry nevertheless is identical in many respects to that of higher plants. Thus, seaweeds are ideal candidates in Carl's estimation for studies involving responses to light at all wavelengths and the uptake of nutrients. Carl has studied most recently the interrelationship of nitrogen and light absorption, using the red alga *Porphyra* as his subject. As available nitrogen in the medium increases, photosynthesis (and subsequent growth) increases. In particular, when nitrogen is in short supply, the nitrogen seems to be shunted to the ultraviolet-absorbing pigments, which Carl attributes to a possible mechanism for enhanced protection of the seaweed. Carl has also noted a dose response. A high level of light to nitrogen-deprived thalli is "deadly." Oxygen metabolism in photosynthesizing plants includes a suite of enzymes to protect against free radical damage. Nitrogen-depleted algae see a drop-off of 70–75% activity of catalase and associated enzymes.

In related experiments with *Laminaria saccharina*, a kelp, Carl

has measured decreased photosynthesis when ultraviolet (UV) light levels are increased in the presence of reduced levels of nitrogen. When protection from UV is provided, photosynthesis increases whether or not levels of nitrogen rise. Photosynthesis increases to maximum levels if nitrogen levels increase. Seaweeds examined from deep-water habitats reach plateaus of photosynthesis at lower light levels than does material taken from shallow-water environments. Different populations of *Laminaria* develop tolerances as a function of their exposure to light, especially UV wavelengths.

Carl made a clear and unambiguous case for his chosen group as candidates for model studies of environmental effects on the health of higher plants and for biochemical studies in simplified systems.

—DON HUDSON, Recording Secretary.

ANNOUNCEMENT

NEW ENGLAND BOTANICAL CLUB
GRADUATE STUDENT RESEARCH AWARD

The New England Botanical Club will offer up to \$2,000 in support of botanical research to be conducted by graduate students in 2002. This award is made annually to stimulate and encourage botanical research on the New England flora, and to make possible visits to the New England region by those who would not otherwise be able to do so. It is anticipated that two awards will be given, although the actual number and amount of awards will depend on the proposals received.

The award will be given to the graduate student(s) submitting the best research proposal dealing with systematic botany, biosystematics, plant ecology, or plant conservation biology. Papers based on the research funded must acknowledge the NEBC's support. Submission of manuscripts to the Club's journal, *Rhodora*, is strongly encouraged.

Applicants must submit four paper copies of each of the following: a proposal of no more than three double-spaced pages, a budget, and a curriculum vitae. Two letters in support of the proposed research, one from the student's thesis advisor, should be sent directly to the Awards Committee by sponsors. All materials should be sent to: Awards Committee, The New England Botanical Club, 22 Divinity Avenue, Cambridge, MA 02138-2020. Proposals and supporting letters must be received no later than March 1, 2002. The recipient(s) will be notified by April 30, 2002.

This year the Graduate Awards Committee is pleased to announce three recipients of the Graduate Student Research Awards. Michael Moody of the University of Connecticut received support for his proposal entitled "Phylogenetics, phenotypic plasticity, and potential hybrids in the aquatic plant genus *Myriophyllum* (Haloragaceae)." The second award was to Valerie Reeb of the University of Illinois at Chicago for her proposal entitled "Phylogenetics of the Acarosporaceae (lichen-forming Ascomycetes) and *Acarospora*, and worldwide revision of the species complex *A. cervina*–*A. glaucocarpa*." The third award was to R. Williams of Michigan State University for the proposal "Phylogeny of *Pycnanthemum* (Lamiaceae) with emphasis on

high-level polyploidy in the *P. virginianum* complex.” For abstracts of these research proposals and a listing of the awards from 1985 to the present, consult the Club’s web page (<http://www.huh.harvard.edu/nebc/>).

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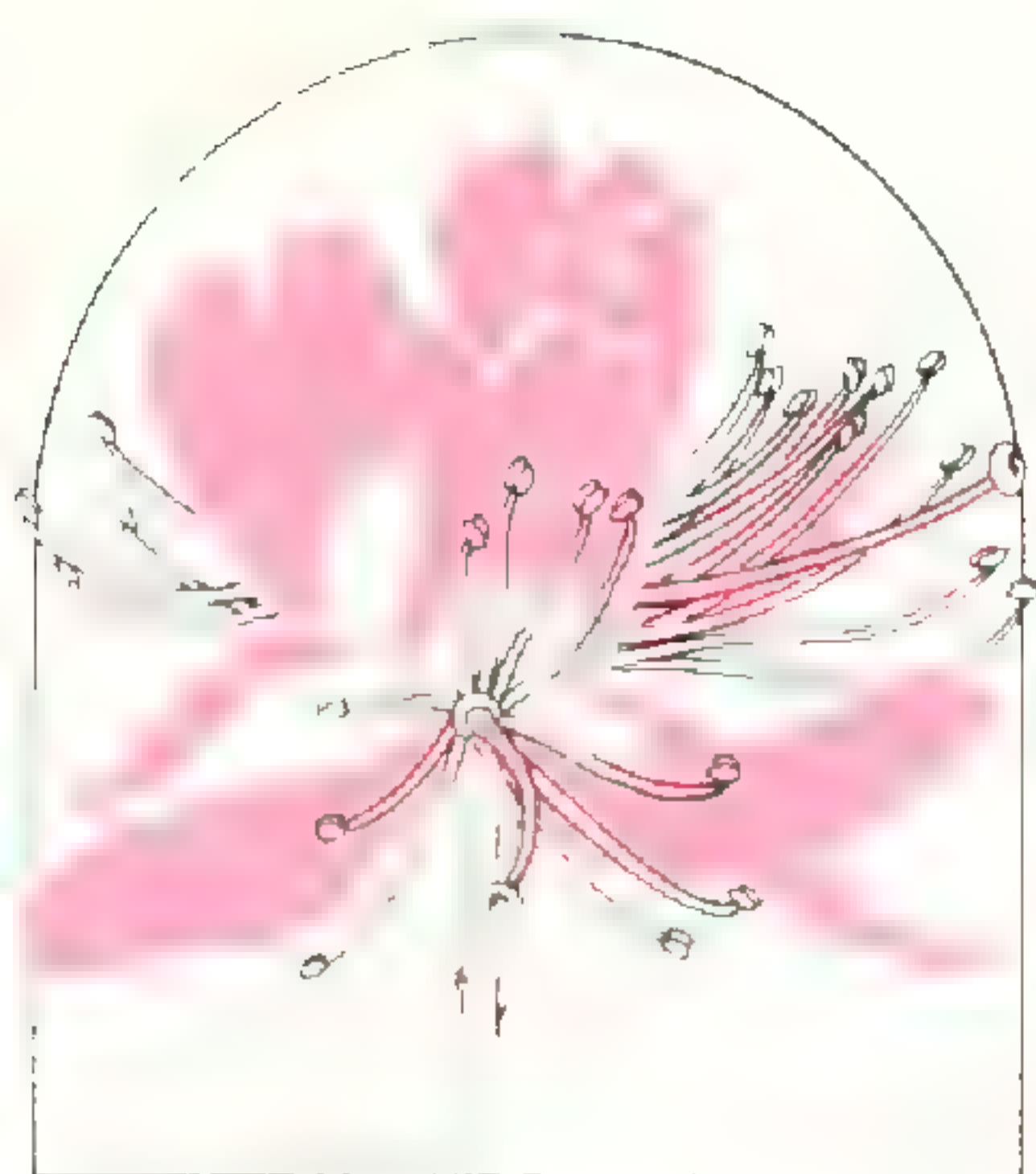
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RHODORA

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CONSERVATION STATUS OF *CAREX ORONENSIS*
(CYPERACEAE), A MAINE ENDEMIC

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ABSTRACT. *Carex oronensis*, Orono sedge, is Maine's only known endemic plant species. From 1916 through 1986 only one individual was collected. From 1986–1998, we and others found 58 populations and approximately 2862 reproductive individuals in early successional habitats, almost exclusively in the Penobscot River drainage. Of extant populations, 80% have < 20 plants, and 22% have only 1–2. In a Principal Coordinates Analysis with 22 morphological variables and 95 individuals, *C. oronensis* separated completely from *C. bebbii*, *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tinctoria*. Canonical Discriminant Analysis resulted in 100% classification for 19 individuals of *C. oronensis*. *Carex oronensis* differs from the four other taxa especially in perigynium features: narrow wings, lack of abaxial nerves, glossy texture, rust-colored blotch (68% of sample), and lack of basal sponginess about the achene. Species status is appropriate for *C. oronensis* because it is fertile, its offspring are identical to the parent, and it is morphologically distinct. Because its distribution is wholly north of the Wisconsin glacial boundary and it is not clearly adapted for long-distance dispersal, the species appears to have arisen in Maine. Hay transport by the lumber industry could account for the spread of *C. oronensis* within the Penobscot River drainage and its confinement there. Mowing after seed dispersal in mid-July appears to benefit populations.

Key Words: *Carex bebbii*, *C. oronensis*, *C. ovalis*, *C. scoparia* var. *tessellata*, *C. tinctoria*, *Carex* section *Ovales*, Cyperaceae, Orono sedge, morphology, Maine, plant endemism, plant conservation

Conservation of species is often prioritized according to endemism, and plant endemism is unusual in northeastern North America (Gentry 1986). *Carex oronensis* Fernald is apparently the only plant species endemic to Maine (Dibble et al. 1989). Two other *Carex* species, *C. elachycarpa* Fernald and *C. josselynii* (Fernald) Mack. ex Pease, were considered narrow endemics (Fernald 1950) until Reznicek and Ball (1979) placed them in synonymy with *C. sterilis* Willd. and *C. echinata* Murray, re-

spectively. Until February 28, 1996, *C. oronensis* was listed in the Federal Register of Endangered and Threatened Plant Species as Category 2, a designation for taxa requiring taxonomic resolution and/or further information about distribution. On that date, Category 2 was eliminated by the U.S. Fish and Wildlife Service because of uneven data quality and insufficient resources to track the more than 3000 species in this category (Office of the Federal Register 1996). *Carex oronensis* was listed as state Endangered due to restricted global distribution (Dibble et al. 1989), but is currently listed as state Threatened because > 50 populations have been documented. It is proposed for state Special Concern due to apparent lack of immediate threats. It is currently considered "S2" and "G2" using the Natural Heritage ranking system (Haines and Vining 1998).

Carex oronensis is a member of section *Ovales* Kunth, the largest section in the genus, in which identification is "notoriously difficult" (Reznicek and Catling 1986) because the numerous species are morphologically similar, gaps between some species are narrow (though deep; A. A. Reznicek, pers. comm.), and for some species groups there has not yet been sufficient taxonomic study to resolve questionable species. Some species apparently intergrade (Whitkus 1988) or hybridize with other species (Fernald 1950; Gleason and Cronquist 1991). The section occurs mostly in temperate North America, with some species in montane regions of Central and South America. Two Eurasian members of section *Ovales*, *C. macloviana* d'Urv. and *C. ovalis* Gooden. (= *C. leporina* L.), are found in North America. The former is unique among *Ovales* in its bipolar distribution (Moore and Chater 1971) and is more or less frequent in Alaska and northwest Canada but is otherwise rarely found in the conterminous United States. *Carex ovalis* is thought to be introduced. In Maine, sect. *Ovales* is represented by 22 species and one variety, more taxa than any other section of the genus (Campbell et al. 1995).

Fernald (1902) named *Carex oronensis* after Orono, the type locale and the town in which he began his botanical activities. Most authors recognize *C. oronensis* at the species level (Fernald 1950; Kartesz 1994). On the other hand, Gleason and Cronquist (1991) suggested that it is a hybrid but specified no putative parents. Early collections of *C. oronensis* were from the southern Penobscot River drainage (Eastman 1980; Figure 1) and date from 1889–1916. Between 1916 and 1986, only one individual

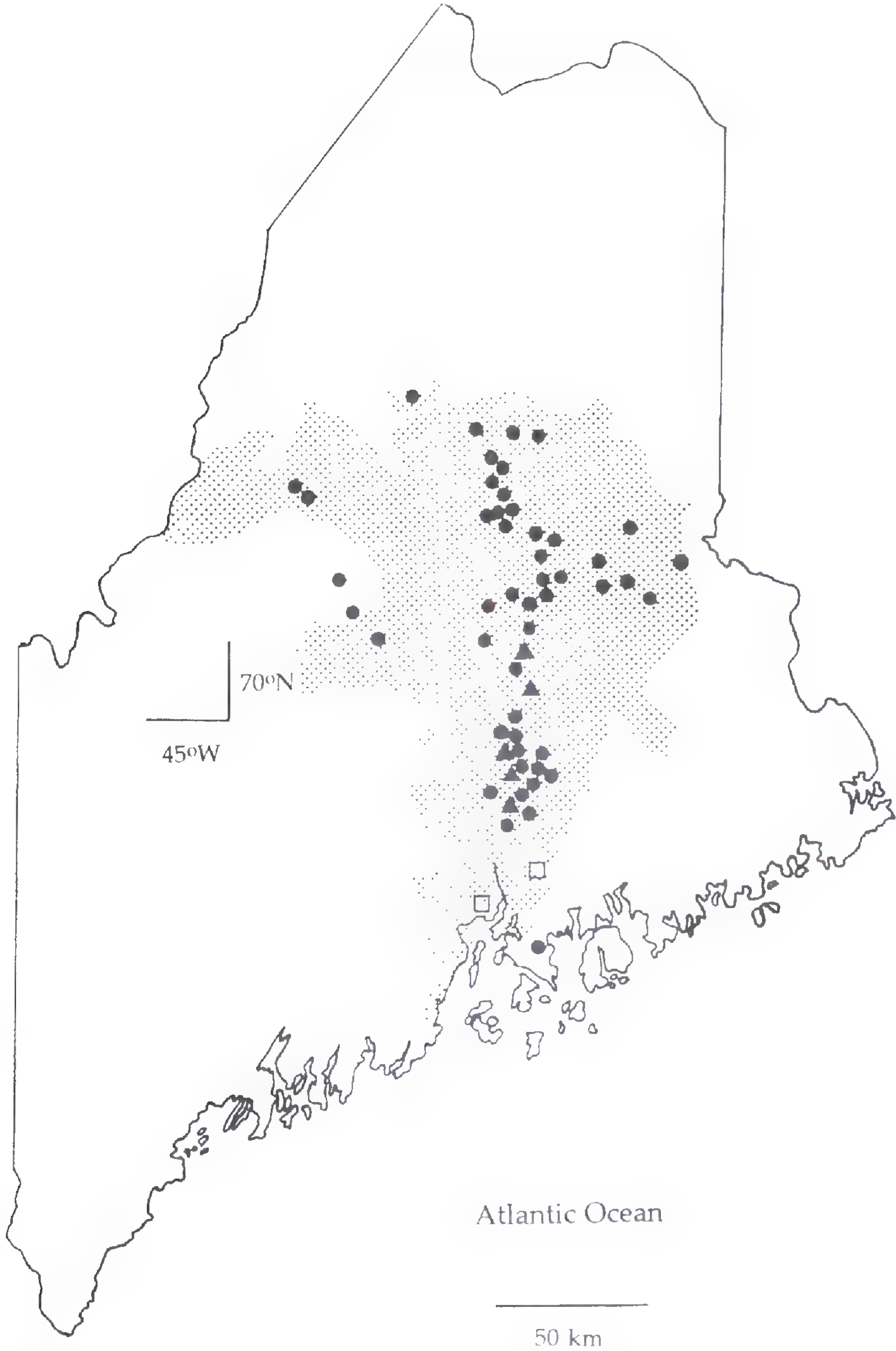


Figure 1. Distribution of occurrences of *Carex oronensis*, all in Maine, U.S.A. showing two unlocated pre-1916 (empty squares) and 53 post-1916 (filled circles) sites. Three of the filled circles represent multiple sites in Orono—where density is highest. Current sites in five townships (filled triangles) could be re-located historic sites, although exact locales for historic collections are unknown. The shaded area is the approximate extent of the Penobscot River drainage.

was collected. Until this study (Dibble 1991), little was known of the morphological distinctness, population size, current distribution, ecology, or reproductive biology for this species.

Our primary objective was to ascertain conservation status of *Carex oronensis*. We sought to determine its geographic distribution, test its morphological distinctness, obtain a chromosome number, characterize its breeding system, describe its habitat, and see with which other members of *Carex* in sect. *Ovales* it grows.

MATERIALS AND METHODS

We conducted field surveys for *Carex oronensis* intensively from 1987–89 and intermittently from 1990–98 within about 80 km of the Penobscot River valley (Figure 1). At each site we collected at least one mature specimen of *C. oronensis* (vouchers at MAINE) and all sympatric members of sect. *Ovales*, and we counted plants of *C. oronensis*, listed associated vegetation, and recorded habitat type. We counted a discrete clump of stems as a *C. oronensis* individual and included only fruiting plants because we cannot identify some members of sect. *Ovales* without mature perigynia.

In a preliminary survey of herbarium material, we examined approximately 600 herbarium specimens, including representatives of all North American and Eurasian species in sect. *Ovales* known to us except *Carex maackii* Maxim. and *C. planata* Franch. & Sav. of Eurasia (Fernald 1950; Gleason and Cronquist 1991; Hermann 1974; Kartesz 1994; Mackenzie 1931–1935) from 14 herbaria (BH, CR, MAINE, MICH, MT, NEBC, NHA, NY, NYS, TRT, UNB, US, VT, and WELC; abbreviations in Holmgren et al. 1990). We also examined approximately 290 specimens we obtained in Maine, New Brunswick, Newfoundland, and Costa Rica. Many of the new collections from Maine and New Brunswick were determined or annotated by P. E. Rothrock and A. A. Reznicek.

Initially we included 12 species in sect. *Ovales* that overlap with *Carex oronensis* in geographic range and that resemble this species in morphology, habit, and habitat requirements. We selected for numerical analysis in the morphological study, those specimens within each taxon that represent the full range of apparent morphological variation. We evaluated 54 characters compiled from taxonomic treatments and from herbarium and field observations, then eliminated 32 characters from the preliminary

data set because of high variability within and considerable overlap among taxa.

The preliminary analysis identified three species—*Carex ovalis*, *C. tincta* Fernald, and *C. bebbii* Olney—and one variety, *C. scoparia* Schkuhr ex Willd. var. *tessellata* Fernald & Wiegand, as morphologically closest to *C. oronensis*. *Carex scoparia* var. *tessellata* has been found in Maine only locally along the coast east of Penobscot Bay. We used only these five taxa in further analysis, with 19 specimens per taxon (Appendix). For *C. ovalis*, we used nine specimens from North America (but not from Maine, where it is rare), nine specimens from Eurasia, and one from New Zealand. Some character states shared by these five taxa (including *C. oronensis*) are loosely cespitose habit (versus densely cespitose or rhizomatous), (3) 4–8 (9) spikes per inflorescence, spike arrangement aggregate (versus moniliform), pistillate scales dark reddish brown with a lighter midvein, and perigynia usually less than 2.5 mm wide. Vegetative characters of *Carex* useful in other studies or floras (Damman 1963; Haines and Vining 1998; Reznicek and Catling 1986; Rothrock 1991; Standley 1989) proved to be of little value in separating *C. oronensis* from the four other taxa in this study. As we could find no vegetative characters that reliably separate these taxa from one another, we included only characters that relate to the inflorescence and associated structures. Limitation of taxonomically useful characters to those associated with the inflorescence in this study parallels work in *Carex* sect. *Montanae* (Crins and Ball 1983). Our study was directed toward distinguishing *C. oronensis* and we did not explore variables that could separate *C. ovalis* and *C. tincta* more definitively. We visually assessed characters using box plots (McGill et al. 1978) in SYSTAT (Version 6.0; SPSS, Evanston, IL). Differences between groups were determined by lack of overlap between the notched portion of boxes on a horizontal axis, and from means and standard deviations.

We scored 10 continuous, 1 discontinuous, and 11 attribute characters (Table 1) for 19 specimens each (total 95) in *Carex bebbii*, *C. oronensis*, *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tincta* (Appendix). The number of populations sampled for each taxon ranged from 10–19. For all characters and most specimens, we used the mean of five replicate measurements per individual (i.e., five different perigynia from one specimen) to account for

Table 1. Twenty-two morphological characters and their states used in the Principal Coordinates Analysis of *Carex oronensis* and four Maine taxa that resemble it. The ten continuous characters (noted as *) were also used in a Canonical Discriminant Analysis. All measurements in mm. “0” indicates absence, “1” presence.

Structure	Character	Character States or Units
Inflorescence	Extent of aggregation	0 – open, the spikelets separate, 1 – tightly aggregate
Pistillate scales	Color	0 – not chestnut-brown, 1 – chestnut-brown
	Length*	mm
	Width*	mm
Perigynium	Length*	mm
	Width*	mm
	Distance from base to widest part*	mm
	Distance from base to first serrulation*	mm
	Beak color	0 – light, 1 – dark
	Beak margin	0 – dark, 1 – hyaline
	Base	0 – without stipe, 1 – substipitate
	Adaxial surface	0 – without blotch, 1 – rust-colored blotch

intraplant variation; single measurements accounted for < 5% of the overall dataset.

For the 95 individuals, we conducted a Principal Coordinates Analysis (PCOR), which is recommended for mixed continuous, discontinuous, and attribute characters, in the NTSYS-PC software (Version 1.8; Exeter Publishing Ltd., 100 North Country Rd., Bldg. B, Setauket, NY 11733), and calculated Gower’s similarity coefficient using the GOWER3 program (T. A. Dickinson, Vascular Plant Herbarium, Royal Ontario Museum, Toronto, ON, Canada). To see how well groups separate on the basis of the 10 continuous characters (Table 1), and to find the most discriminating of these characters, we conducted Canonical Discriminant Analysis (CDA) with stepwise variable selection in SYSTAT. We examined the continuous characters in an ANOVA and post hoc multiple comparisons using Tukey’s Studentized Range (HSD) test ($\alpha = 0.05$) with Bonferoni adjustments.

To determine chromosome number, we fixed inflorescence buds of *Carex oronensis* in the early morning in Farmer’s Solution

Table 1. Continued.

Structure	Character	Character States or Units
Achene	Texture of adaxial surface	0 – dull, 1 – pearly
	Wing tooth color	0 – light, 1 – dark
	Adaxial surface	0 – nerves weak, 1 – nerves prominent
	Abaxial suture margin	0 – light, 1 – hyaline adaxial
	Nerves	Count
	Base of achene	0 – not surrounded by spongy tissue, 1 – spongy
	Wing width*	mm
	Length*	mm
	Width*	mm
	Stipe length*	mm

(3:1 absolute alcohol:acetic acid, by volume) for 24 hr. and stored them at 5°C in 70% ethanol. We squashed anthers and stained with acetocarmine. Chromosome counts were obtained from cells in late prophase I using a Zeiss Standard microscope.

We tested for self- and cross-compatibility using seven individuals of *Carex oronensis* and two each of *C. tincta* and *C. tenera* Dewey, which we dug from natural populations, mostly in Orono, and maintained as potted individuals in a greenhouse. To determine if these species were self-compatible, we bagged intact inflorescences prior to anther dehiscence on three individuals of *C. oronensis* and one each of *C. tincta* and *C. tenera*. Seeds from open pollinations of *C. oronensis* were planted in a common garden to determine whether the species would breed true.

To test pollen viability in five *Carex oronensis* individuals, we immersed fresh pollen from five anthers per plant in two drops of Alexander’s (1969) pollen stain on a glass slide and examined after 2 min. at ×1600. We counted more than 200 grains for each sample. Red-staining pollen grains were counted as unaborted, and those that stained green were considered aborted. As stainability does not necessarily indicate germinability, we also germinated fresh pollen from five anthers each for four individuals of *C. oronensis* on glass slides in two drops of germination medium (agar, 2.5 g; H₂O, 250 ml; sucrose, 107 g; CaNO₃, 0.07 g; Boron, 0.07 g; adapted from Stanley and Linskens 1974) for 24 hr. at room temperature and then examined for germinability at

×1600. We scored more than 200 pollen grains per sample for pollen tube growth.

We germinated open-pollinated seeds from five individuals of *Carex oronensis* in the light on moist filter paper following six weeks of cold storage at 5°C. We used frequency of filled achenes as an estimate of fruit set in five individuals of *C. oronensis* selected from different parts of the species range, with a sample of 28 flowers per individual.

RESULTS

Morphological study. We determined that no species in *Carex* section *Ovales* from Mesoamerica or from western or south-eastern North America was as close morphologically to *C. oronensis* as species from northeastern North America and Eurasia. We found *C. oronensis* to be a distinct entity and we present a description based on our measurements (see below). In an ordination plot of the first and second Principal Coordinates based on 22 variables, *C. oronensis* and *C. bebbii* each separated well from *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tincta* (Figure 2). The failure of these latter three taxa to form distinct clouds was not because they were difficult to distinguish from each other but because we emphasized characters that differentiated *C. oronensis*. Higher dimensions failed to resolve *C. oronensis* and were otherwise relatively uninformative. The first two Principal Coordinates accounted for 31.5 and 26.6%, respectively, of the total variation in the original variable space, or a total of 58.1%. *Carex oronensis* is closest to *C. ovalis* and *C. tincta*. These latter two did not separate on the basis of the characters examined.

Canonical Discriminant Analysis on seven continuous characters selected by stepwise analysis resulted in perfect classification of *Carex oronensis* and *C. bebbii* (Table 2). The other three taxa classified at least 80% correctly, with three individuals of *C. ovalis* classifying as *C. tincta*. Plots of various combinations of the first three canonical axes failed to show a discrete cloud for any taxon but *C. oronensis* (not shown).

Carex oronensis differed markedly from *C. bebbii*, *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tincta* (Figure 3) in perigynium width, perigynium wing width, and achene stipe length (Table 3; Figures 4d, 4h, 4l). The number of perigynium abaxial nerves was higher in *C. oronensis* than in the other taxa (Figure 4g).

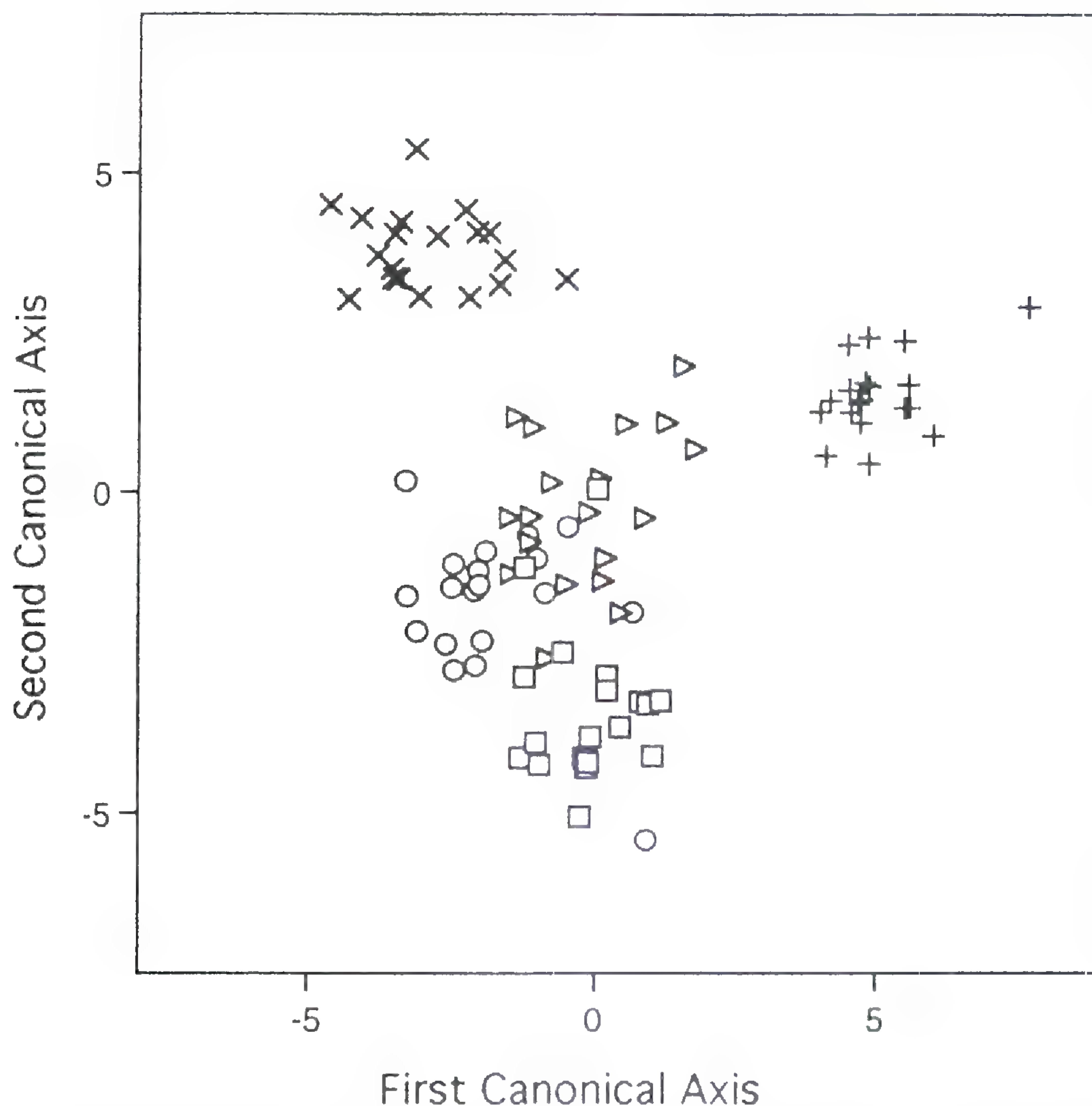


Figure 2. Plot of Principal Coordinates Analysis for 22 morphological characters and 19 specimens each of *Carex bebbii* (+), *C. oronensis* (x), *C. ovalis* (circle), *C. scoparia* var. *tessellata* (square), and *C. tinctoria* (triangle).

Carex oronensis differed from at least one other taxon in 11 of the 12 quantitative variables (Figures 4a–4l, but not 4i). *Carex oronensis* and *C. tinctoria* differed from the other three taxa in perigynium scale length (Figure 4a). *Carex oronensis*, *C. tinctoria*, and *C. ovalis* were distinguished from *C. bebbii* and *C. scoparia* var. *tessellata* in perigynium scale width (Figure 4b), perigynium length (Figure 4c), and distance from the base of the perigynium to the first serrulation (Figure 4f). Achene width was similar in *C. oronensis*, *C. bebbii*, and *C. scoparia* var. *tessellata* (Figure 4k).

In addition to the narrow perigynium and short achene stipe of *Carex oronensis* (Table 3), qualitative characters we found useful

Table 2. Canonical loadings, discriminant function (a), and table of frequencies (b) for classifying *Carex bebbii*, *C. oronensis*, *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tinctoria* based on seven morphological characters.

Character	Canonical Loadings		Discriminant Function				
	1	2	<i>bebbii</i>	<i>oronensis</i>	<i>ovalis</i>	<i>tessellata</i>	<i>tinctoria</i>
Constant			-106.07	-185.70	-213.39	-198.82	-175.76
Pistillate scale length	0.84	0.18	22.93	34.74	39.86	34.64	25.10
Pistillate scale width	-0.51	-0.38	68.11	105.06	94.62	83.24	93.59
Perigynium length	-0.61	0.44	35.33	44.69	42.75	52.96	43.74
Distance from base of perigynium to wing serrulation	-0.36	-0.34	-3.37	-1.54	0.16	-15.19	1.63
Distance from base to widest part of perigynium	-0.30	0.18	-5.35	-9.46	-10.67	-6.50	-9.65
Perigynium wing width	0.24	0.57	-21.39	-82.93	-313.84	-28.10	-27.41
Achene width	0.14	0.07	-10.38	-30.06	-11.04	-21.06	-5.21

Table 2. Continued.

b) Frequencies, showing observed (rows) and predicted (columns) number of individuals classified, with percent in parentheses. Correct classifications in bold.

Taxon	<i>bebbii</i>	<i>oronensis</i>	<i>ovalis</i>	<i>tessellata</i>	<i>tincta</i>	Total
<i>bebbii</i>	19 (100%)	0	0	0	0	19
<i>oronensis</i>	0	19 (100%)	0	0	0	19
<i>ovalis</i>	0	0	15 (80%)	1	3	19
<i>tessellata</i>	0	0	0	18 (95%)	1 (5%)	19
<i>tincta</i>	1 (5%)	0	0	0	18 (95%)	19
Total	20	19	15	19	22	95

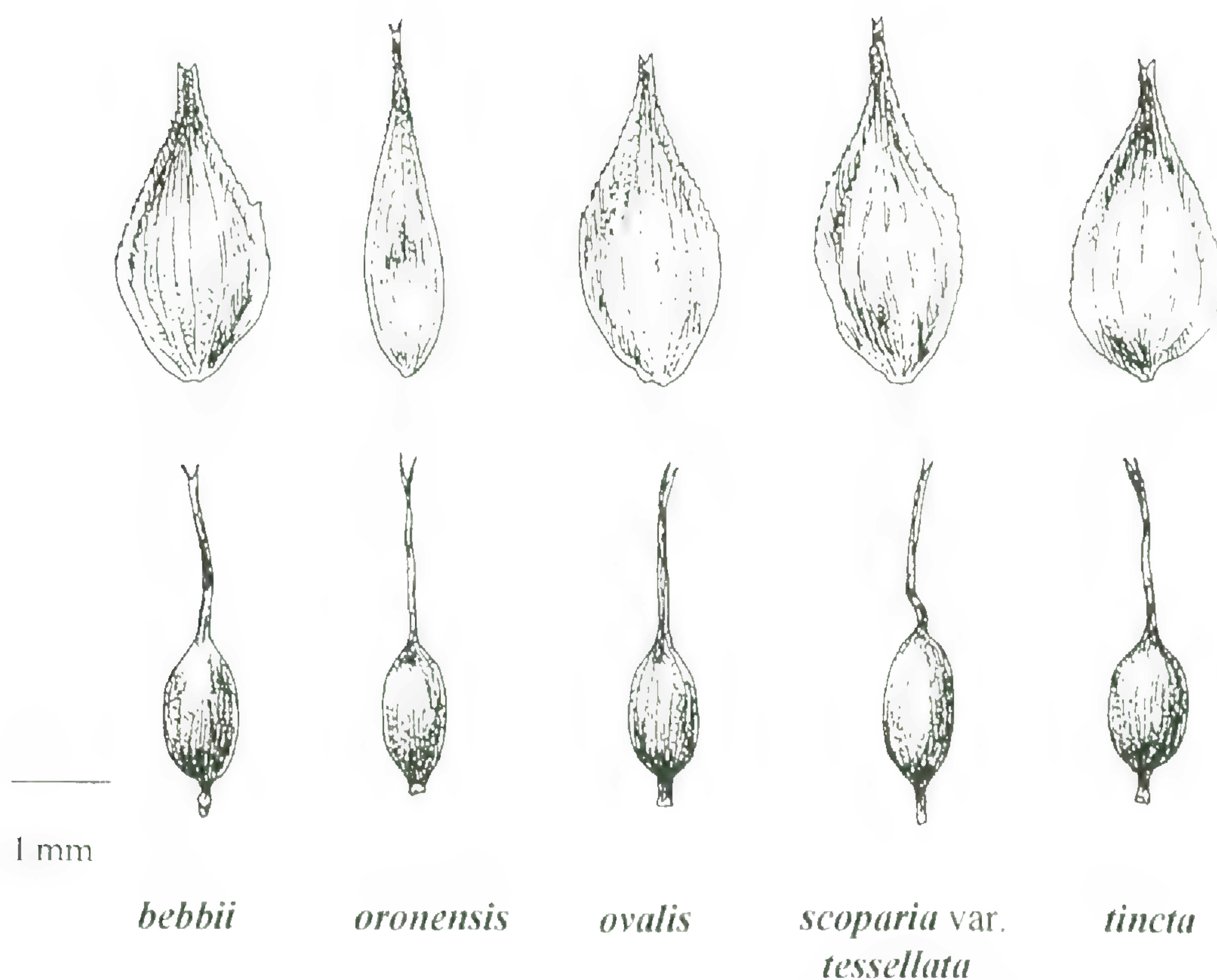


Figure 3. Perigynia and achenes of *Carex bebbii*, *C. oronensis*, *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tinctoria*.

for separating this species from the other four taxa included absence of a wing below the middle of the perigynium, pearly appearance of the perigynium adaxial epidermis, lack of prominent adaxial perigynium nerves, presence (in 68% of our sample) of a rust-colored blotch on the perigynium adaxial epidermis, and lack of spongy thickening on the inside wall of the perigynium at the base of the achene (Table 4). Mature perigynia are required to distinguish *C. oronensis* from *C. ovalis* or *C. scoparia* var. *tessellata*. In the upcoming *Flora of North America* treatment of *Carex*, the distance from achene summit to beak apex is 1.2–2 mm in *C. ovalis*, and greater than 2 mm in *C. scoparia* var. *tessellata* (A. A. Reznicek, pers. comm.). We did not include this variable in our study, and this might have contributed to the failure of these two taxa to separate well in Figure 2. In the field these three Maine *Ovales* are distinctive for their dark scales that almost equal the perigynium in length. Characters especially useful for distinguishing *C. oronensis* in the field are perigynium width, texture, and rusty blotch when present.

Table 3. Mean $\pm$ SD (range) for quantitative variables that distinguish *Carex oronensis* from *C. bebbii*, *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tineta* [Tukey's Studentized Range (HSD) test]. Lengths and widths in mm. Means within a row followed by the same letter are not significantly different ($P = 0.05$). N = 19 for each taxon. * = distance from base to maximum width along axis. † = count variable, thus Tukey multiple comparisons of means not appropriate.

Character	Taxon				
	<i>bebbii</i>	<i>oronensis</i>	<i>ovalis</i>	<i>tessellata</i>	<i>tineta</i>
Scale length	2.66 $\pm$ 0.17 a (2.34–2.94)	3.48 $\pm$ 0.22 b (3.06–3.85)	4.07 $\pm$ 0.33 c (3.33–4.48)	3.73 $\pm$ 0.22 d (3.32–4.12)	3.32 $\pm$ 0.28 b (2.63–3.72)
Scale width	0.89 $\pm$ 0.10 a (0.69–1.12)	1.24 $\pm$ 0.09 b (1.02–1.40)	1.31 $\pm$ 0.12 b (1.11–1.52)	1.05 $\pm$ 0.11 c (0.87–1.26)	1.26 $\pm$ 0.15 b (0.83–1.57)
Perigynium length	3.08 $\pm$ 0.22 a (2.75–3.49)	3.71 $\pm$ 0.26 b (3.25–4.12)	4.08 $\pm$ 0.29 b (3.60–4.56)	4.39 $\pm$ 0.31 c (3.58–4.89)	3.85 $\pm$ 0.32 b (3.18–4.36)
Perigynium width	1.29 $\pm$ 0.10 a (1.04–1.47)	1.10 $\pm$ 0.11 b (0.88–1.30)	1.73 $\pm$ 0.17 c (1.45–2.05)	1.83 $\pm$ 0.10 c (1.57–1.96)	1.72 $\pm$ 0.21 c (1.20–1.99)
Perigynium distance*	1.14 $\pm$ 0.15 a (0.92–1.58)	1.32 $\pm$ 0.19 b (0.86–1.66)	1.45 $\pm$ 0.19 b (1.10–1.94)	1.52 $\pm$ 0.17 b (1.28–1.92)	1.47 $\pm$ 0.16 b (1.12–1.78)
Perigynium ab. nerves†	5.2 $\pm$ 1.6 (1.2–7.4)	10.40 $\pm$ 1.26 (8.40–12.60)	7.50 $\pm$ 1.53 (3.60–9.75)	6.05 $\pm$ 1.62 (0.80–8.80)	6.56 $\pm$ 1.12 (3.40–8.40)

Table 3. Continued.

Character	Taxon				
	<i>bebbii</i>	<i>oronensis</i>	<i>ovalis</i>	<i>tessellata</i>	<i>tincta</i>
Distance to serrulation	1.13 ± 0.18 a (0.78–1.56)	1.52 ± 0.20 b (1.00–1.84)	1.69 ± 0.26 b (1.20–2.16)	1.24 ± 0.19 c (0.98–1.64)	1.62 ± 0.15 b (1.32–1.86)
Wing width	0.23 ± 0.55 a (0.15–0.35)	0.10 ± 0.22 b (0.06–0.16)	0.31 ± 0.08 a (0.23–0.58)	0.36 ± 0.07 a (0.25–0.49)	0.28 ± 0.08 a (0.12–0.44)
Tooth length	0.04 ± 0.01 a (0.03–0.09)	0.03 ± 0.01 a (0.02–0.05)	0.04 ± 0.01 a (0.03–0.06)	0.04 ± 0.01 a (0.02–0.05)	0.04 ± 0.01 a (0.03–0.08)
Achene length	1.10 ± 0.05 a (0.93–1.18)	1.46 ± 0.08 b (1.27–1.64)	1.44 ± 0.08 b (1.32–1.57)	1.37 ± 0.04 b (1.30–1.45)	1.40 ± 0.06 b (1.29–1.50)
Achene width	0.68 ± 0.05 a (0.56–0.79)	0.85 ± 0.12 a (0.62–1.26)	1.02 ± 0.12 b (0.76–1.29)	0.77 ± 0.03 a (0.72–0.83)	0.99 ± 0.15 b (0.79–1.30)
Stipe length	0.40 ± 0.05 a (0.29–0.48)	0.29 ± 0.06 b (0.10–0.35)	0.54 ± 0.09 c (0.31–0.64)	0.54 ± 0.12 c (0.18–0.64)	0.38 ± 0.08 a (0.20–0.55)

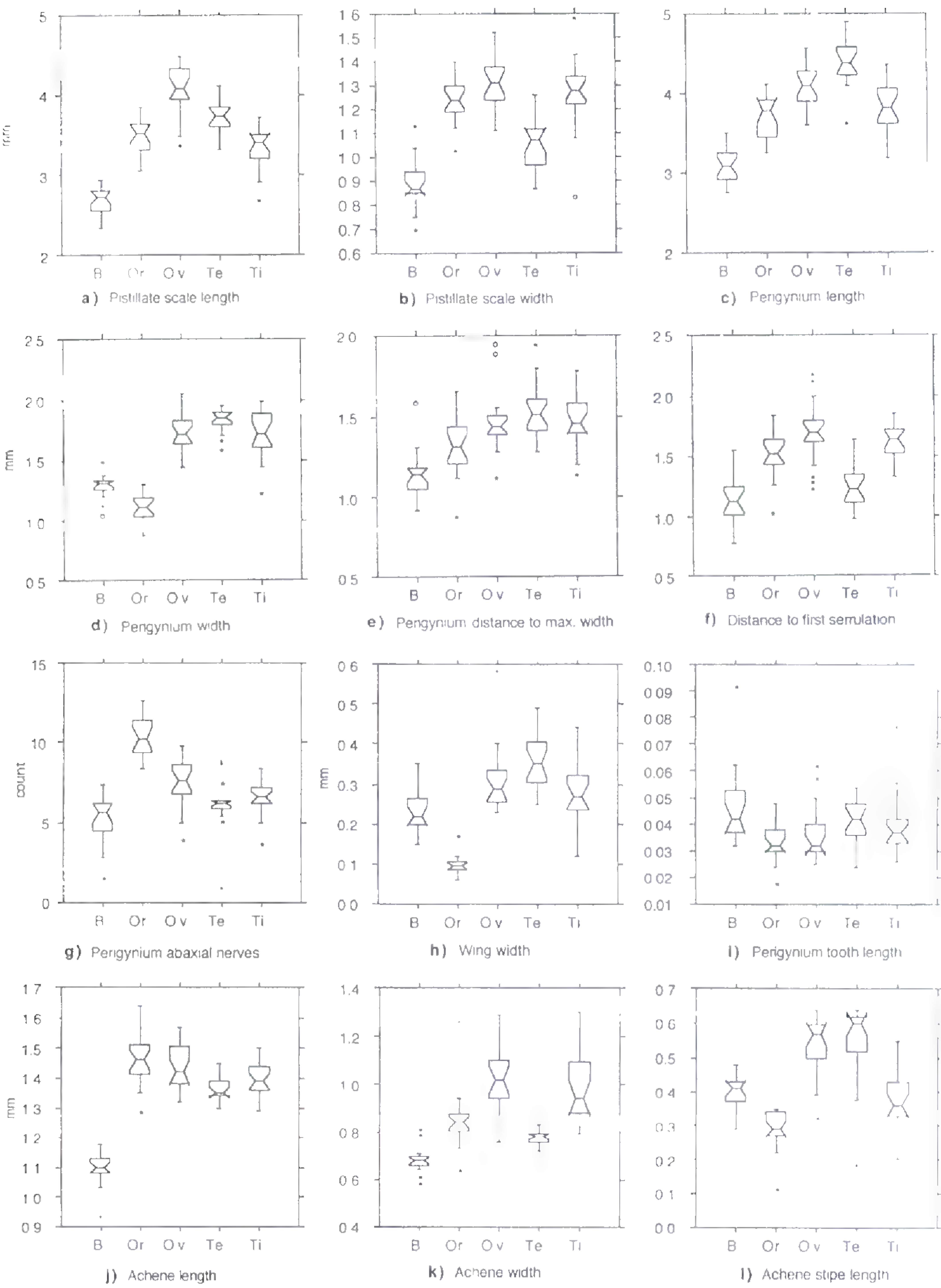


Figure 4. Notched box plots of five *Carex* species and 12 quantitative variables for reproductive structures listed in Table 1. B = *C. bebbii*, Or = *C. oronensis*, Ov = *C. ovalis*, Te = *C. scoparia* var. *tessellata*, Ti = *C. tinctoria*.

Table 4. Summary of morphological characters that distinguish *Carex oronensis* and four taxa that resemble it.

Character	Taxon				
	<i>bebbii</i>	<i>oronensis</i>	<i>ovalis</i>	<i>tessellata</i>	<i>tincta</i>
Mean perigynium width	1.3 mm	1.1 mm	1.7 mm	1.8 mm	1.7 mm
Pistillate scale length in relation to perigynium	Shorter	(Usually) subequal	Subequal	Shorter	Shorter
Wing below middle of perigynium	Present	Narrow or lacking	Present	Present	Present
Texture of adaxial surface of perigynium	Dull	Pearly	Dull	Dull	Dull
Adaxial nerves	Strong	Usually weak	Strong	Strong	Strong
Number of abaxial nerves	4–7	8–15	4–10	1–9	3–9
Rust-colored blotch on perigynium adaxial surface	Absent	Present in ca. 88%	Absent	Absent	Absent
Sponginess at base of achene within perigynium	Present	Absent	Present	Present	Present
Achene stipe length	Long	Short	Long	Long	Intermediate

Carex tinctoria was often 20–40 cm taller than *C. oronensis* and *C. ovalis*, with a thicker stem, fewer fertile culms per individual, wider spikes, fewer flowers per spike, perigynium beak visible above the shorter scales, and the perigynium adaxial surface usually flattened. Also, its perigynia were almost completely dispersed by late July, while *C. oronensis* often retained a few perigynia in the spike through the succeeding winter. Perigynia in *C. tinctoria* were usually sessile, while those of *C. oronensis* and *C. ovalis* were usually short-stalked.

Carex bebbii differed from the other species in this study in its more tightly aggregated inflorescence, compact spikes, short and narrow pistillate scales, shorter distance from the base to the widest part of perigynium, and tendency to occur in wetter habitats. This species was sympatric with *C. oronensis* along a gravelly railroad landing, a site that is uncharacteristic for *C. bebbii* in Maine; this suggests that the amplitude for habitat preference in *C. bebbii* might be greater than often assumed.

Other taxa in sect. *Ovales* that occur within the range of *Carex oronensis*, and with which it might be confused, include *C. crawfordii* Fernald and *C. tribuloides* Wahlenb. Both have as narrow a perigynium, but both differ from *C. oronensis* in leaf width, scale color, scale length and width, perigynium shape and texture, achene dimensions, and, in *C. crawfordii*, style configuration (contorted versus straight in *C. oronensis*). *Carex foenea* Willd. (syn. *C. aenea* Fernald) occasionally has a long bract subtending the inflorescence, its scales equal or exceed perigynia in length, and the perigynia are larger, darker, and have more prominent nerves than those of *C. oronensis*, *C. ovalis*, or *C. scoparia* var. *tessellata*. The achenes of *C. foenea* are dark brown when ripe, while those of the other three taxa are light to medium brown.

Geographical distribution, population size, and habitat characteristics. During field surveys conducted between 1987–98, we and others located 58 populations and 2862 individuals of *Carex oronensis*; this expanded the known range by more than 100 km in several directions (Figure 1). All populations occurred in the Penobscot River drainage except for two small populations in the adjacent Kennebec drainage (most sites listed in Dibble 1991).

Plant size and population density (counted number of individuals per estimated area at each site) were greatest in mesic mead-

ows in full sun. The largest populations of *Carex oronensis* were within 2 km of the Penobscot River in old hay fields that were mowed every few years. Distribution of population size was strongly skewed toward small populations. Eighty percent of extant populations had fewer than 20 individuals, 22% had only one or two individuals, and only two populations contained more than 300 individuals.

Carex oronensis occurs in open habitats on various soil types from sand to fine silt loam—the “argillaceous meadows” of Fernald’s herbarium labels from 1916. Habitats include hay fields, old fields, sandy roadsides, powerlines, borders of cultivated fields, edges of commercial and residential establishments, rivershore, gravel pits, swales, woods roads, an alluvial oak forest, and a former sawmill site. Soil moisture ranges from seasonally inundated to dry. Elevation is not known to exceed 360 m and slope ranges from none to 30%. Occurrences are often surrounded by apparently suitable habitat not occupied by *C. oronensis*.

Associated vegetation. For 49 of the 58 *Carex oronensis* populations, we found a total of 10 other species in sect. *Ovales*, with varying numbers of sites at which they were found [*C. bebbii* 1, *C. crawfordii* 8, *C. foenea* (formerly *C. aenea*) 1, *C. merritt-fernaldii* Mack. 2, *C. normalis* Mack. 3, *C. projecta* Mack. 9, *C. scoparia* var. *scoparia* 20, *C. tenera* 13, *C. tinctoria* 13, and *C. tribuloides* 4]. *Carex scoparia*, *C. tenera*, and *C. tinctoria* were the most common sympatric species and these are common throughout much of the range of *C. oronensis*, especially on roadsides. We did not observe *C. scoparia* var. *tessellata* or *C. ovalis* growing with *C. oronensis*, and we have not often found *C. ovalis* in Maine. *Carex* in sections other than sect. *Ovales* that were common in *C. oronensis* sites included *C. gracillima* Schwein. and *C. pallescens* L. Other associated vegetation includes many non-native (according to Campbell et al. 1995; Haines and Vining 1998), early successional herbs such as *Rumex acetosella* L., *Leucanthemum vulgare* Lam., *Ranunculus acris* L., *Anaphalis margaritacea* (L.) Benth. & Hook. f., *Achillea millefolium* L., *Phleum pratense* L., *Trifolium* spp., *Vicia cracca* L., and *Hieracium* spp. Native associates include *Juncus* spp., *Luzula* spp., *Panicum* spp., *Solidago* spp., *Rubus idaeus* L., *Apocynum androsaemifolium* L., *Salix* spp., and *Spiraea alba* Du Roi var. *latifolia* (Aiton) Dippel.

Table 5. Percent fruit set, seed germination, pollen stainability, and pollen germination in *Carex oronensis*. N = number of individuals.

Character	N	Sample per Individual	Percent		
			Mean	SD	Range
Fruit set	5	28 flowers	90.6	5.4	80.3–97.2
Seed germination	5	97, 53, 42, 83, 70	27.7	36.5	8.2–92.8
Pollen stainability	5	>200 grains	88.5	5.4	79.5–94.2
Pollen germination	4	>200 grains	70.0	17.4	51.6–90.0

Reproductive ecology and results of compatibility experiments. *Carex oronensis* is usually protogynous, but anthers dehisce within a few days of stigma receptivity and stigmas and anthers are often presented simultaneously. Anthesis occurs from late May to mid-June, overlapping that of many sympatric *Carex* species but often preceding *C. tinctoria* by one to two weeks. Anthesis and fruit maturation can occur at the same time within an individual, but later flowers are smaller and less likely to yield fruits. Mean fruit set, pollen germination, and pollen stainability equalled or exceeded 70%, while seed germination averaged 27.7% (Table 5). Controlled self-pollinations and intraspecific crosses of *C. oronensis* yielded at least some viable seeds per inflorescence. Open-pollinated seed of *C. oronensis* planted in the common garden produced offspring indistinguishable from *C. oronensis*. Casual observations suggest dispersal by wind, water, and gravity from late June through October and in early spring.

We counted the haploid chromosome number for *Carex oronensis* as $n = 34$ in multiple cells in one individual (voucher for population Dibble 72, see Appendix; voucher for this same individual, Dibble 10020, 1 Jul 2001, MAINE).

DISCUSSION

Conservation of *Carex oronensis* would be difficult or impossible if it was not morphologically distinct. Our results clarify and reinforce Fernald's (1902, 1950) perception of this as a discrete entity. One character not mentioned by Fernald that is useful when present is the rust-colored blotch on the adaxial surface of the perigynium. Few eastern North American *Ovales* feature this, even occasionally. Some western North American *Ovales* bear a

rust-colored blotch, but our sample size was too small to determine whether this is consistent throughout the range of such taxa. Of the specimens with a rust-colored blotch that we examined, only *C. oronensis* consistently lacked basal sponginess about the achene.

We have seen a few populations of *Carex oronensis* disappear since we first found them, though the seed bank might hold this species. Small populations are not unusual in many *Carex* species (Richards 1986), and Reznicek (1986) usually found Mexican and Central American *Carex* in sect. *Hymenochlaenae* in predominantly small, widely dispersed populations.

Nineteenth century loggers may have influenced the distribution of *Carex oronensis* through the practice of supplying hay (containing seed of *C. oronensis*) to logging camps within the same watershed where trees were harvested, with little commercial exchange between watersheds. The two *C. oronensis* populations that occurred outside the Penobscot River drainage were along a former supply route to the West Branch of the Penobscot River. The presence of these populations in the Kennebec River drainage could be explained by hay shipments from the Bangor area (in the lower Penobscot River drainage) along Moosehead Lake (in the upper Kennebec River drainage) to Pittston Farm (in the upper West Branch of the Penobscot River drainage), which is a former supply center for loggers on the West Branch and a current site for *C. oronensis*. This method was suggested for the eastward expansion of *C. praegracilis* W. Boott along railways (Reznicek and Catling 1987). Similarly, *C. crawfordii* was introduced to Great Britain from North America with crop seed (Jermy et al. 1982). The proximity of *C. oronensis* to the Penobscot River or one of its tributaries may also reflect some habitat conditions that we have not yet recognized or quantified.

The chromosome count for *Carex oronensis* was $n = 34$ in our study, and $n = 37$ in Rothrock and Reznicek (1996a). It is not known whether this variation is due to aneuploidy, which is prevalent in *Carex* and thought to influence speciation in this genus (Grant 1981). There is an opportunity for recombination through agmatoploidy, in which chromosome fragments retain viability because of the diffuse centromere (Davies 1956), and such fragments of chromosomes are capable of surviving from one generation to the next (Rothrock and Reznicek 1996a). Variation in chromosome number within species may be considerable in sect.

Ovales (Whitkus 1991). Agmatoploidy presumably may decrease or increase chromosome number (Reznicek 1990). Chromosome number may vary among cells of one individual or more often at intra- and interpopulation levels in some species in sect. *Ovales*. However chromosome number in *Carex* is generally considered stable, so such variation could be due to misidentification of taxa in at least some cases (Whitkus 1991).

Status and possible origin of *Carex oronensis*. *Carex oronensis* deserves species status because it is morphologically distinct, has a well-defined geographic range, bears fertile seed and pollen, and has the ability to breed true. We found no intergradation between this species and any other.

Carex oronensis, with $n = \text{ca. } 34, 37$, could have resulted from chromosome breakage in *C. ovalis* ($n = 32, 33$, and 34 ; all counts from Europe), *C. tinctoria* ($n = 36 + \text{IV}$ from one plant only; Rothrock and Reznicek 1996a), or *C. scoparia* var. *tessellata* ($n = 33$ from several sites; P. E. Rothrock, pers. comm.).

While polyploidy and hybridization are known in *Carex* (Cayouette and Catling 1992; Grant 1981) and sect. *Ovales* (Rothrock and Reznicek 1996b; Rothrock et al. 1997), our data do not support the suggestion that *C. oronensis* is of hybrid origin. Fernald (1950) claimed hybridization among six species, not including *C. oronensis*, within eastern North American members of sect. *Ovales*. *Carex* hybrids are often sterile (Eaton 1957; Whitkus 1988), but sterile or poorly developed individuals that are not hybrids are also fairly frequent in *Carex* whether or not the species is self-compatible (A. A. Reznicek, pers. comm.). Such depauperate individuals could result from disease, herbivory, or insufficient pollination due to adverse weather during anthesis. We found three sterile individuals that are morphologically more or less intermediate (in features other than filled achenes, which were lacking) between *C. oronensis* and *C. tinctoria* and one sterile intermediate between *C. oronensis* and *C. scoparia*; all were from the largest known population, which is in Orono. We could not assign parentage to numerous sterile individuals from a site in Carroll where *C. oronensis* was present. Otherwise, we encountered few apparent hybrids for which *C. oronensis* is a possible parent.

Firm evidence regarding the nonhybrid origin of *Carex oronensis* is lacking, but the plausibility of various hypotheses can

be considered. If *C. oronensis* is a relict whose formerly widespread distribution has been reduced by climate change, as with some serpentine-adapted *Carex* endemics (Waterway 1990), then we would expect the distribution to include widely disjunct populations. Paleoendemism seems unlikely for *C. oronensis* because it is confined to an area that was recently covered by glacial ice and its apparently suitable habitat is widely distributed.

We speculate that limited distribution in a recently glaciated region, and relatively narrow intraspecific variation in morphology, suggest that *Carex oronensis* is a young taxon. A single evolutionary event could have led to divergence from an unidentified parent since the Laurentian ice shield receded about 13,000 years ago. A scenario suggested to us informally by A. A. Reznicek (pers. comm.) is plausible: during the pleistocene *C. oronensis* might have been restricted to sandy river terraces, and these gradually became forested. The agricultural activities of early native Americans and later of European settlers led to an expansion of early successional habitat near rivers. In the 18th and 19th centuries, river impoundments might have altered the sandy river bar and terrace habitat; this could have led to association of *C. oronensis* more with human disturbance than with river dynamics. Recently, dispersal of *C. oronensis* could be through transport of hay. Lack of dispersal beyond two river drainages in Maine could be due to some biological feature that limits colonization by *C. oronensis*, such as low germination rate or seedling survival rate under natural conditions, or a short life span that prevents dissemination of many propagules over a period of years. We know of no data to support these suggestions.

Ovales of the southeastern United States have been studied by Rothrock and Reznicek (1996b). Derivation from a species of that region, during or following the maximum extent of the Wisconsin glacier, seems unlikely because *Carex oronensis* is morphologically dissimilar to such taxa. Derivation from *Ovales* of western North America, including species from potential refugia in the Rocky Mountains and near the Pacific Coast, appears improbable because *C. oronensis* does not resemble them, either. It does share morphological features with two Eurasian *Ovales*: *C. ovalis* and *C. macloviana* (which grows in North America as well, and differs from *C. oronensis* especially in its metallic appearance of the perigynia, presence of spongy tissue at base of achene, and fewer abaxial nerves on the perigynium). Both of these Eurasian taxa

have dark scales that equal or exceed the perigynium in length; however, both lack the narrow perigynium of *C. oronensis*. The perigynium of *C. macloviana* is distinctly longer and wider than that of *C. oronensis*.

Carex oronensis could have arisen from *C. ovalis*, a weedy species of Europe (Kukkonen and Toivonen 1988). As with some other plants adventive to North America (Faden 1989; Reznicek and Catling 1987), arrival time, place, and means are unknown. Fernald (1902) thought that *C. ovalis* was “doubtless introduced” in New Jersey but was “perhaps indigenous northward,” or “naturalized from Europe” (Fernald 1950). The earliest collection in North America that we have seen is that of W. Boott from Long Island, Boston Harbor, Massachusetts in 1871 (NY). *Carex ovalis* was divided into at least three subspecies, but these were rarely applied to North American collections and are no longer recognized (Chater 1980; Jermy et al. 1982). Some Eurasian specimens show marked variation and differ morphologically from North American *C. ovalis* in habit, plant height, number of spikes per culm, and in other features of the inflorescence, although perigynia approximate those of North American *C. ovalis*.

Definitive identification of a closest relative or parent taxon for *Carex oronensis* may require a molecular study including much of sect. *Ovales*. Morphology, chromosome numbers, reproductive biology, and habitat preferences will enhance such a study but cannot, in themselves, be used to assign relatedness for this species.

Implications for conservation and management of *Carex oronensis*. Because *Carex oronensis* is a distinct taxon (see description), with a well-defined geographical distribution and ephemeral habitat in the absence of human intervention, management recommendations are straightforward. Given the intensity of habitat disturbance with which this species is associated, populations could be short-lived and difficult to conserve unless mowed or perhaps burned on an annual or biennial schedule. Ideally, such treatment would be conducted after seeds have dispersed, thus no sooner than late July. Further field survey might reveal that mowing obscures populations and maintains them in a vegetative state, and more populations are likely to be found. Field checks for most of the 58 known sites have not been conducted since they were first observed in the late 1980s, and no

demographic studies have been undertaken. There are no data regarding dispersal capability, fecundity, survivorship, longevity of individuals, and persistence of populations. This globally rare taxon is currently without any regulatory protection on either the federal or state level. Only four of the 58 known populations are on public lands and there, habitat is kept open by mowing or by timber harvest activities in the vicinity. Additional research regarding phylogeny and population viability could provide a better picture of relatedness and assure that, where protection can be undertaken, this species does not reach irrecoverably low population size.

DESCRIPTION

Carex oronensis Fernald, Proc. Am. Acad. 37: 471. 1902.

LECTOTYPE designated here: UNITED STATES. Maine: Orono, dry fields, etc. [*sic*], 30 Jun 1891, *Fernald s.n.* GH! (Originally identified by Fernald as “*Carex scoparia* Schk. forma”).

Plants loosely caespitose; roots black, fibrous. Fertile culms 30–100 cm, exceeding leaves in height, scabrous below the inflorescence. Cauline leaves 3–4 per fertile culm, 2–4 mm wide. Inflorescences 1.5–3.4 × 0.6–1.5 cm; spikes aggregate, usually (3) 5–6 (10), gynecandrous, 5–10 × 3–7 mm, each spike with 14–36 pistillate and 6–12 staminate flowers. Pistillate scales acute to acuminate or rounded, nearly equal to perigynia in length, 3.1–3.9 × 0.9–1.6 mm, chestnut-brown, glossy, with pale midvein and hyaline margins. Perigynia lanceolate or oblanceolate, light green to straw-colored, usually bearing a rust-colored blotch on adaxial surface, 2.9–4.3 long × 0.9–1.4 mm wide, wingless below the middle, wings slightly toothed toward apex, with adaxial epidermis pearly in appearance, usually lacking prominent nerves or with 5–7 obscure nerves, abaxial nerves 7–15; beak tip to top of achene 1.5–2.4 mm; beak tip hyaline; ventral suture usually with hyaline margin; spongy tissue at base of achene lacking. Achenes light brown, body 1.3–1.6 × 0.7–1.4 mm; achene stipe 0.2–0.4 mm long; style straight; stigmas 2, red-brown. $n = 34, 37$.

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APPENDIX

SPECIMENS USED IN MORPHOLOGICAL STUDY

Carex bebbii Olney

UNITED STATES. Maine: Aroostook Co., Houlton, Carey's Mills, near Meduxnekeag River in low wet area, 30 Jun 1988, *Dibble* 945 (MAINE); Linneus, Rt. 2A, dooryard of old farmstead, 7 Jul 1988, *Dibble* 1324 (MAINE); Penobscot Co., Bangor, Air National Guard Base W of city, roadsides, 19 Jul 1991, *Dibble* 3693 (MAINE); Holden, Hog Hill, logging road upper NE slope, 17 Jul 1992, *Dibble* 4137–4138 (MAINE); Masardis, in gravel at RR track, site of old RR station, 6 Jul 1988, *Dibble* 1280 (MAINE); Orono, swale, 27 Jun 1891, *Fernald* s.n. (NHA); Orono, Rt. 2, gravel near RR track, 5 Jul 1991, *Dibble* 3664 (MAINE); Orono, Rt. 2, gravel near RR track, 10 Jul 1992, *Dibble* 4139–4142 (MAINE); Prentiss, Rt. 169, roadside bank, 1 Jul 1988, *Dibble* 970 (MAINE); Piscataquis Co., Dover, low thicket, 15 Jul 1895, *Fernald* 284 (L. A. Standley). Massachusetts: Berkshire Co., Monterey, unshaded fen along Konkapot River, 4 Jul 1991, *Rothrock* 2342 (MAINE); Essex Co., W. Manchester, railroad side, 30 Jun 1911, *Hubbard* 61a (MAINE). Michigan: Kalamazoo Co., Kalamazoo, brushy marsh, 23 Jun 1992, *Rothrock* 2518 (MAINE); Vicksburg, black muck soil in willow swamp/dogwood thicket, 25 Jun 1982, *Rothrock* 1605 (MAINE). Pennsylvania: Centre Co., State College, calcareous swamp with *Typha* and *Carex stricta*, 1 Jul 1975, *Rothrock* 615 (MAINE).

Carex oronensis Fernald

UNITED STATES. Maine: Aroostook Co., Haynesville, roadside, 7 Jul 1988, *Dibble* 1312 (MAINE); Molunkus, dooryard of former homestead, 13

Jul 1987, *Dibble 143* (MAINE); Sherman, edge of potato field, 1 Jul 1988, *Dibble 1176* (MAINE); Penobscot Co., Bangor, compost heap at Mt. Hope cemetery, 22 Jun 1988, *Dibble 1073* (MAINE); Carroll Plantation, North Rd., King Farm, old field, 5 Jul 1988, *Dibble 1246* (MAINE); Medway, Rt. 11 along E. shore, East Branch, Penobscot River, vacant lot in residential area, 13 Jul 1987, *Dibble 146* (MAINE); Old Town, alluvial woods on banks of Stillwater River in old gravel pit, dry sandy soil, 12 Jul 1987, *Dibble 121* (MAINE); Orono, type locality, argillaceous meadows, 27 Jun 1916, *Fernald 152*, PLANTAE EXSICATTAE GRAYANAE (MICH); Orono, roadside SW jct. Stillwater Ave. and Forest Ave., 22 Jun 1988, *Dibble 1062* (MAINE); Orono, Gardner Rd., old field, 3 Jul 1987, *Dibble 72* (MAINE); Passadumkeag, E shore Penobscot River, rocky rivershore, 30 Jun 1988, *Dibble 1163* (MAINE); Prentiss, old fields, roadside, jct. Rt. 171 and shortcut W to Rt. 170, 1 Jul 1988, *Dibble 1173* (MAINE); Winn, Rt. 2, roadside, dry soil, 13 Jul 1987, *Dibble 139* (MAINE); T3 R7 WELS, Hunt Farm, opening at roadside, E shore, East Branch, Penobscot River, 1 Jul 1988, *Dibble 1181* (MAINE); T 4 Indian Purchase, woods road E of North Twin Lake, 28 Jun 1988, *Dibble 1157* (MAINE); Piscataquis Co., Monson, Rt. 6/15, hayfield, 28 Jun 1989, *Dibble 2200* (MAINE); T6 R9 WELS, Trout Brook Farm, Baxter State Park, open meadow to N of ranger cabin, 6 Jul 1988, *Dibble 1257* (MAINE); T7 R11 WELS, Pinkham Rd. NE of Carpenter Mt., roadside, 23 Jun 1989, *Dibble 2151* (MAINE); Somerset Co., T2 R4 NBKP, Pittston Academy Grant, Pittston Farm, old fields near Penobscot River to NE of farmstead, 28 Jun 1989, *Dibble 2208* (MAINE).

Carex ovalis Gooden.

ARMENIA (Transcaucasia). distr. Nor. Bajazet, 3 Aug 1928, collector unknown (NY).

CANADA. New Brunswick: Carleton Co., Woodstock, roadside ditch along Trans Canada Hwy., 25 Jul 1988, *Dibble 1600* (MAINE); York Co., Fredericton, The Hermitage, terrace above St. John River, 25 Jul 1988, *Dibble 1615*, *Hinds & Rooney* (MAINE). Newfoundland: Cape Ray, woods near Table Mt., 7 Jul 1912, *Curtis 21-18-20-221* (MAINE).

FRANCE. Moniturts Basin, Alps, Ch. d'Allerzette, 16 Jul 192?, collector unknown (MICH).

GERMANY. Mecklenburg, 14 Aug 1987, *Siering s.n.* (MICH).

NEW ZEALAND. Thomas River, Canterbury, Jan 1 1973, *Thompson 370* (MICH).

NORWAY. Ved Vrietiania, 1883, *Duhl s.n.* (BH).

SPAIN. LaRioja: Logrono, Iberica San Millan de la Cogolla, prado humados 1800 m, 29 Jul 1987, *Luceno & Vargas 2446* (MICH); Lusitania: Lameiro da Quinta do Rio Frio, Arredores da Guarda, 12 Jun 1949, *Fernandes & Lausac s.n.* (BH).

SWEDEN. "Suburb of Stockholm", 3 Jul 1949, *Ohlsen s.n.* (NY).

UNITED STATES. Maine: Aroostook Co., Orient, Rt. 1 at Weston town line, 7 Jul 1988, *Dibble 1335* (MAINE); Penobscot Co., Carroll Plantation, North Rd., King Farm, swale in old field, 5 Jul 1988, *Dibble 1247* (MAINE); Orono, low pasture, 22 Jul 1916, *Fernald & Long 1296* (NHA); Oxford Co., Canton, dry rocky pasture, 21 Jun 1908, *Parlin s.n.* (MAINE). Massachusetts:

Norfolk Co., Dedham, dry field, 4 Jul 1907, *Bartlett* 792 (MICH). New Hampshire: Rockingham Co., Hampton Falls, Newfound Hill, 17 Jun 1900, *Easton s.n.* (MICH). North Carolina: Mitchell Co., Roan Mt., edge of trail in fir wood on summit, ca. 6200 ft., 11 Jul 1959, *Hermann* 15209 (MICH).

USSR. Leningrad region, 25 Jul 1964, *Chater s.n.* (MICH).

Carex scoparia Schkuhr ex Willd. var. *tessellata* Fernald & Wiegand

UNITED STATES. Maine: Hancock Co., T 9 SD, bottom of moist sandy borrow pit, 11 Jul 1995, *Dibble* 4816 & *Rothrock* (MAINE); Penobscot Co., Prentiss, 1 Jul 1988, *Dibble* 1199, (MAINE); Washington Co., Addison, sandy roadside, 22 Jul 1995, *Dibble* 4818 (MAINE); Columbia Falls, sandy roadside, 22 Jul 1995, *Dibble* 4815 (MAINE); Jonesport, in Sphagnum moss next to freshwater pond NE of Sandy River Beach, 7 Jul 1993, *Lewis s.n.* (Univ. Maine at Machias Herbarium); Jonesport, Sandy River Beach, 17 Jul 1992, *Reznicek* 9154 (MAINE); Machias, Cross Rd., swale along roadside, with *C. scoparia*, 23 Jul 1988, *Dibble* 1592 (MAINE); Pembroke, dry low ground, 8 Jul 1909, *Fernald* 1464 (NY); Roque Bluffs, 23 Jul 1988, *Dibble* 1588-1591, 1593, 1596, 1597, 2400 (MAINE); Unionville, sandy roadside at edge of blueberry field, 11 Jul 1995, *Dibble* 4817, 4819 & *Rothrock* (MAINE). New York: Long Island, Montauk, sandy shores at Great Pond or Point, 4 Jul 1927, *Latham* 4146 (NY).

Carex tinctoria Fernald

CANADA. Alberta: Fort Saskatchewan, in "grassy slough", 11 Sep 1956, *Turner* 9430 (MICH). New Brunswick: North Co., confluence Miramichi and Renous River, dry bank, 22 Jun 1978, *Hinds & Breen* 481 (UNB); York Co., Nortondale, West Branch, Nackawic Str., dry roadside at swampy woods at jct. Rt. 585/Rt. 595, 25 Jun 1982, *Hinds* 6005 (UNB). Ontario: Thunder Bay, lakeshore at Roundtable Lake, 18 Jul 1951, *Garton* 1440 (NY).

UNITED STATES. Maine: Aroostook Co., Fort Fairfield, dry soil, 12 Jul 1893, *Fernald* 165 (L. A. Standley); Fort Fairfield, roadside, 1 Jul 1940, *Chamberlain* 1702 (MAINE); Haynesville Ferry Bridge, roadside, 7 Jul 1988, *Dibble* 1311 (MAINE); Hersey, roadside bank, Rt. 11, 6 Jul 1988, *Dibble* 1255 (MAINE); Mapleton, dry field, 12 Jun 1941, *Chamberlain* 2618 (MAINE); Presque Isle, roadside swamp, Washburn Rd., 1 Jul 1939, *Chamberlain* 1139 (MAINE); Penobscot Co., Carroll Plantation, North Rd., King Farm, swale in old field, 5 Jul 1988, *Dibble* 1234 (MAINE); Charleston, wet ditch by roadside, 4 Jul 1905, *Knight s.n.* (MICH); Medway, dry soil, Rt. 11, vacant lot, 13 Jul 1988, *Dibble* 147 (MAINE); Orono, dry soil, 12 Jul 1890, *Fernald* 1231 (MAINE); Piscataquis Co., Monson, Rt. 6 hayfield, old field, 28 Jun 1989, *Dibble* 2201 (MAINE); Somerset Co., T2 R4 NBKP, Pittston Academy Grant, Pittston Farm, old fields near Penobscot River to NE of farmstead, 28 Jun 1989, *Dibble* 2207 (MAINE). Massachusetts: Hampshire Co., Middlefield, hillside meadow, 26 Jun 1913, *Fernald & Long* 8982 (NY.). New Hampshire: Coos Co., Jefferson, meadow, 3 Jul 1950, *Pease s.n.* (NHA). Vermont: Caledonia Co., St. Johnsbury, meadow, 2 Jun 1901, *Hazen* 206 (VT).

A ROLE FOR WATER DROPLETS IN THE POLLINATION
OF *PLATANTHERA AQUILONIS* (ORCHIDACEAE)

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ABSTRACT. The North American *Platanthera aquilonis* Sheviak has long been known to autopolinate. Pollinia rotate forward and downward out of the anther sacs and contact the stigma. Previous experimental evidence has indicated that this movement is effected by gravity. In addition to the movement of whole pollinia, flowers are often found in which continuous streams of pollen massulae emanate from anther sacs and seemingly pour down onto the stigma. Experiments with cultivated plants have shown that water droplets can collect in the centers of flowers of this species. These sometimes draw a sheet of massulae out of an anther sac either onto the surface of the droplet or into its interior. As the droplet evaporates, the massulae are deposited as a continuous layer from the anther sac onto the stigma. It is suggested that in nature dew may function to produce the observed pollen streams.

Key Words: *Platanthera aquilonis*, *Platanthera hyperborea*, pollination

The recently described *Platanthera aquilonis* Sheviak is a widespread and well-known North American species that has been confused with the Icelandic *P. hyperborea* (L.) Lindl. (Sheviak 1999). Autogamy in the North American species has long been known, having been reported [as *Habenaria hyperborea* (L.) R. Br.] by Asa Gray (1862a, 1862b). Shortly after the flower opens, or sometimes while still in the bud, the weak caudicle bends and the pollinia are said to fall onto the stigmatic surface below (Gray 1862a, 1862b; Catling 1983; Catling and Catling 1991). Catling (1983) determined that the motion evidently is driven by gravity, as it did not occur in experimentally inverted flowers.

My experience with cultivated plants of *Platanthera aquilonis* largely confirms these earlier findings. In plants from across much of the range of the species, from Alaska to Illinois and New York, a bending of the caudicle rotates the pollinium forward through a longitudinal fissure in the anther sac and downward onto the stigma. This process may be evident in newly opened flowers or may be delayed for several days. A common feature of plants in the field, however, and clearly evident in the herbarium, suggests

that an additional process is at work. The pollinia are very loosely organized (again as reported by Gray 1862b), with massulae (i.e., primary groups of pollen tetrads) only weakly bound secondarily into easily fragmented pollinia. Quite commonly, loose massulae emanate from anther sacs still enclosing the remnants of pollinia and trail down onto the stigma. How this condition arises has not previously been reported; evidence suggesting a plausible causative agent is presented here.

MATERIALS AND METHODS

A number of plants of *Platanthera aquilonis* from various sites across the range of the species have been maintained in cultivation for many years. They are grown in a modern office building under a motorized track-mounted 1000-watt metal halide lamp. The area has been used for over 20 years to grow plants of various species of *Platanthera*, *Spiranthes*, and other genera. Conditions are suitable for maintenance of normal phenotype expression, and many individual plants have survived throughout this period. In 1997 one plant of *P. aquilonis* from Illinois (McHenry Co., Sheviak 5599), and in 1999 two plants from New York (Essex Co., Sheviak 6229) were employed in experiments. Temperatures were maintained within a few degrees of 20°C, but humidity varied widely.

In 1997 the Illinois plant produced a large inflorescence, and flowers opened over a period exceeding one month in length. Despite this protracted interval, near the end of the period no flowers had been pollinated and all pollinia remained enclosed within the anther sacs. In the several years of cultivation of plants of this species, this was the first case noted in which autopollination had not occurred. The humidity in the growing area at that time was uniformly quite low, so I suspected that the anther sacs might have been unusually rigid, thereby trapping the pollinia. This provided an unusually clear opportunity to investigate the possible role of humidity in pollination, since autopollination was not occurring by any means, and humidity could be readily manipulated.

In the initial trial in 1997, a very fine mist of water from a hand pump atomizer was directed at the inflorescence of the Illinois plant, and the plant was enclosed in a colorless transparent plastic cylinder closed at the top but open at the bottom to permit

limited air exchange yet retain humidity. The walls of the cylinder were also sprayed to create a humid chamber. The chamber was removed for the night, and, following some initial positive response that was evident the following morning, the misting was repeated. In 1999 verification was attempted, and the same procedure was repeated on the two New York plants.

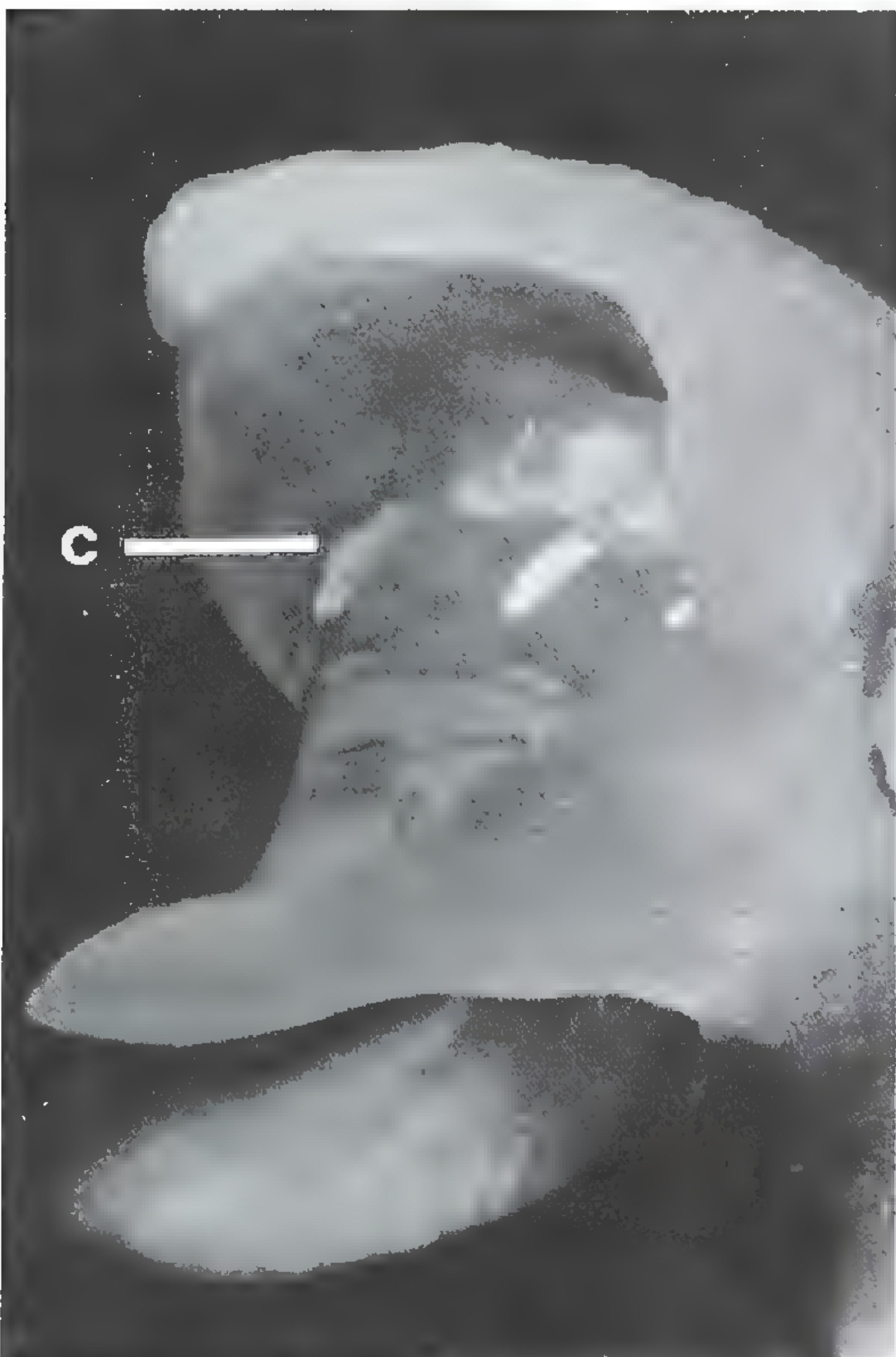
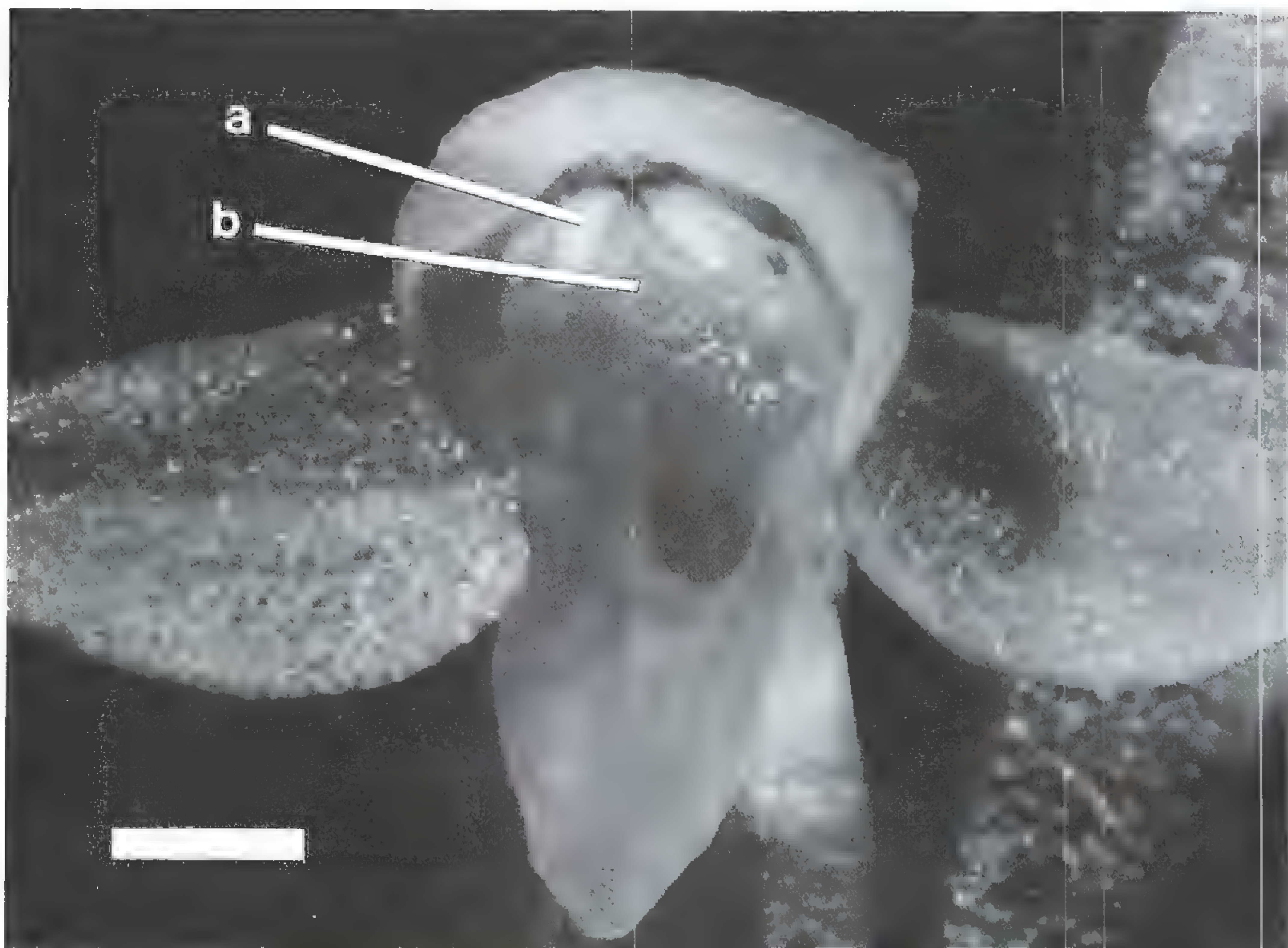
RESULTS

With the first misting of the Illinois plant, numerous very small drops of water formed on the floral segments. In many cases these immediately coalesced to form a single large drop that occupied the center of the flower, immersing the column. After 90 minutes the water had evaporated from the flowers. At that time there was no noticeable change in the flowers, but the following morning several pollinia were found to be protruding from the anther sacs; one was nearly completely free of the sac. With the second misting, drops again formed in the centers of the flowers. In several flowers, within 30 minutes of application, the massulae were drawn out onto the surface of the water droplet as if pulled by the surface tension. As the water evaporated, the pollen maintained its position. Eventually, following the complete evaporation of the water, the pollen remained, forming a continuous sheet from the surface of the stigma to the remains of the pollinium within the anther sac.

The New York plants were misted within a few days of the flowers' opening. At that time pollinia were already appearing and a few flowers had been pollinated. The flowers this time proved to be more hydrophobic than in the preceding example, with the result that water tended to drip off of the flowers rather than be drawn into them. Nonetheless, some drops did form in the centers of flowers. The results in these cases were somewhat



Figure 1. One of the flowers of *Platanthera aquilonis* from New York showing autopollination effected by a central water droplet. All to same scale; scale bar = 1 mm. Top: Front view before treatment. Pollinia (white bodies) are fully exposed within the open anther sacs; a – pollinium (one of two); b – stigma. Lower left: Oblique view showing central water droplet (note arching reflections on surface of droplet). c – Pollinium on the left is free of the anther sac and is riding on the surface of the droplet; pollinium on the right



is partially fragmented with massulae dispersing on the droplet surface. Lower right: Front view after evaporation of the water. The massulae of the left pollinium are dispersed across the stigma. Most of the right pollinium remains within the anther sac, but a stream of massulae extends from the sac down across the stigma.

different than in the preceding trial. In most cases whole pollinia were drawn into the drop, or sometimes onto its surface. Only rarely did massulae stream out, and then sometimes this occurred within the drop rather than on its surface. Examples are shown in Figure 1. With the evaporation of the drop, whole pollinia were deposited on the stigma, or in some cases within the mouth of the spur or even on a floral segment. In those few cases where separated massulae emanated from the anther sac, a sheet of pollen was deposited across the stigma. The massulae in these plants appeared more tightly bound together than in the Illinois plant, with the result that the pollen was not deposited so evenly as in that case.

DISCUSSION

These results bring to mind the cases of *Liparis loeselii* (L.) L. C. Rich., a common associate of *Platanthera aquilonis*, and the tropical *Oeceoclades maculata* (Lindl.) Lindl. In these species, however, the actual impact of raindrops has been implicated in pollination. In *Liparis*, the drops have been found to physically dislodge partially exposed pollinia (Catling 1980), and in *O. maculata*, the impact apparently removes the anther cap and permits the pollinia to hang near the stigma, where another, undetermined agent effects actual pollination (González-Díaz and Ackerman 1988).

The very limited trials reported here indicate a plausible origin for the pollen streams that had previously been noted on *Platanthera aquilonis* flowers in the field and herbarium. Additionally, these trials account for the placement of pollinia on perianth surfaces and within spurs, as has also sometimes been seen. In *P. aquilonis* any wetting of the inflorescence that leads to formation of droplets in the centers of the flowers may facilitate pollination. The coalescence of very small droplets into larger central ones that was seen in the present experiments suggests that dew might commonly function in this capacity. Rain might also in some cases be effective, but it was not simulated during this study; the hooded perianth and its rather hydrophobic surfaces may tend to deflect raindrops. Less common meteorological conditions, such as blowing fog or mist, might function similarly to dew, but they would not be expected to be significant except in certain areas where they were common phenomena.

The frequency of suitable droplet formation would be expected to vary with the habitat, and the relative influence of gravity- and water-assisted pollination may vary accordingly. Certainly the latter is lacking unless water is present, but it may be important in areas with frequent dew formation during anthesis. Furthermore, partially offsetting the positive effects of droplet formation is pollen loss through deposition in spurs and on perianth surfaces. Hence, in areas where dew is frequent during anthesis, incoherent pollinia might represent part of a water pollination syndrome subject to selection through increased pollination and reduced loss of pollinia. In this regard, it may be significant that the Illinois plant, with its very loosely associated massulae, was from an open wet prairie where dew formation was likely a common occurrence. In contrast, the New York plants were found in a dense forest of *Tsuga canadensis* Carrière with *Acer saccharum* Marshall on a rather dry hillside; in such a situation dew formation is probably an uncommon occurrence, and the less fragile pollinia of these plants may reflect a prevalence in this population of gravity-assisted rotation and a rarity of water pollination.

This speculation on possible evolutionary significance of these observations is based on a very small sample and obviously a larger and geographically more diverse sample is necessary for verification. Further study of this novel pollination mechanism, especially in natural populations occurring under diverse conditions, might prove valuable. In addition to gravity- and water-assisted autopollination, the flowers retain the structures necessary for insect pollination, thus suggesting a third dimension that might be important in some situations. *Platanthera aquilonis* thus may be a significant subject for study of the evolution of pollination mechanisms.

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GENDER-RELATED DIFFERENCES IN GAS EXCHANGE
RATES IN THE GENDER-SWITCHING SPECIES
ARISAEMA TRIPHYLLUM (ARACEAE)

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ABSTRACT. Females in dioecious species are generally expected to have higher rates of photosynthesis than are males of the same species. This sexual dimorphism is believed to evolve to compensate for higher costs of reproduction in females relative to males. However, some studies have shown that males in dioecious species have higher rates of carbon assimilation than females. The current study measures photosynthetic rates in males and females of the same genotype in the gender-switching species, *Arisaema triphyllum*. Males were found to have higher photosynthetic rates on a per unit area basis. However, females had greater overall carbon assimilation rates because of their significantly greater leaf area. Photosynthesis in the current study was measured at flowering; presumably developing embryos were not acting as carbon sinks at this time. *Arisaema triphyllum* has a corm (an underground storage organ) that may be the primary sink for carbon. A regression including only females reveals a significant inverse relationship between pseudostem diameter (a proxy for corm size) and photosynthetic rate; as corm size increased, the photosynthetic rate decreased. This suggests that in very large females having greater stored resources, the corm is not as strong a sink as it is for smaller females, at least during the flowering phase of the growing season. For smaller females however, photosynthetic rates do appear to be sink-limited. There was no relationship between corm size and photosynthetic rates among males. Overall, males and females appear to have different patterns of assimilation, at least early in the growing season.

Key Words: photosynthesis, gender switching, carbon assimilation, sexual dimorphism, *Arisaema triphyllum*, Araceae

Dioecious plant species have male (pollen-bearing) and female (ovule-bearing) reproductive phases on separate individuals. In some species, dioecy is known to be genetically controlled (Barlow and Wiens 1975, 1976; Mulcahy 1967; Schink and Mechelke 1989; Warmke 1946; Westergaard 1946; Ye et al. 1991), while in others, gender expression is labile (Schlessman 1988). Among both dioecious and sexually labile species, females have often

been found to allocate more of their resources to reproduction than males (Clay 1993; Dawson and Ehleringer 1993; Dawson et al. 1990; Gross and Soule 1981; Lloyd and Webb 1977; Lovett Doust et al. 1986).

Greater allocation to reproduction among females is thought to provide evidence of a higher cost of reproduction for females relative to males. This pattern of allocation is consistent with Bateman's principle, which suggests that female reproductive success is limited by resources while male reproductive success is limited by mate availability (Bateman 1948). In response to differential reproductive costs, sexual dimorphism appears to have evolved in many morphological as well as physiological traits. Sexual dimorphism may be found in overall plant size and floral display, in life history traits, and in general patterns of resource allocation to reproduction versus growth and survival. As a result of allocation strategies thought to have evolved in response to higher female reproductive costs, females with high reproductive effort may have lower survival rates than males, may grow more slowly than males, and may have a lower reproductive potential than males following a reproductive episode (Lloyd and Webb 1977).

In addition to tradeoffs in allocation to reproduction versus growth and survival, sexually dimorphic patterns in physiological traits related to carbon acquisition have also been observed. In general, females of dioecious species are thought to have greater inherent photosynthetic rates relative to males of the same species (reviewed in Dawson and Geber 1999; Delph 1999) to compensate for higher reproductive costs. When photosynthesis is sink limited, differences between the assimilation rates of males and females may arise as a result of increased sink strength, driven by maturing fruits, for example (Dawson and Bliss 1989; Delph 1999; Delph and Meagher 1995). In some studies, however, males have been shown to have higher overall rates of photosynthesis than females (Gehring and Monson 1994; Laporte and Delph 1996; Marshall et al. 1993). Moreover, Marshall et al. (1993) found that nonreproductive individuals had the same photosynthetic rates as females. Marshall et al. (1993) suggested that male reproduction may cost more than female reproduction in *Phoradendron juniperinum* Engelm. ex A. Gray because of the abundant pollen production, while Delph and Meagher (1995) suggested that males may have a higher overall carbon cost related

to architectural differences between males and females in *Silene latifolia* Poiret. Although males in *S. latifolia* have nearly twice the dark respiration rate of females, they still fix 50% more carbon than fruiting females (Laporte and Delph 1996). Delph (1999) pointed out that understanding the basis of physiological differences between males and females may be important to understanding relative costs of reproduction.

Gender-changing species such as *Arisaema triphyllum* (L.) Schott, Jack-in-the-pulpit, offer an unusual opportunity for exploring the relationship between gender expression and photosynthetic capacity. Unlike dioecious species that have been studied previously, genotypic differences in photosynthetic capacity can be completely controlled in *A. triphyllum*. In gender-changing species, individuals may exhibit either the male or female phase, usually depending on size. In *A. triphyllum*, nonreproductive individuals are the smallest individuals in a population, while males tend to be intermediate in size and females are always the largest individuals (Bierzychudek 1982, 1984; Ewing and Klein 1982; Lovett Doust and Cavers 1982; Lovett Doust et al. 1986; Policansky 1987; Schaffner 1922; Vitt 1997). In addition, vegetative reproduction is common in natural populations, allowing for comparisons of physiological traits between individuals that differ in gender but not genotype.

While the relative costs of reproduction for males and females of this species remain unknown, *Arisaema triphyllum* has many traits that suggest that reproduction is energetically more expensive during the female phase: females are always larger, on average, than males within the same population (Bierzychudek 1982; Ewing and Klein 1982; Policansky 1987; Vitt 1997); gender in one year has a significant effect on gender in the subsequent year with males more likely to become female than females are to remain female in the next season (Vitt 1997); females that produce fruit are more likely to be male or vegetative in the subsequent season than are females without fruit (Policansky 1987); larger females produce more flowers, fruits, and seeds than smaller females, and successful fruit and seed maturation is positively correlated with plant size (Lovett Doust et al. 1986); females devote a greater portion of dry weight to reproductive structures than do males (Lovett Doust and Cavers 1982); and females have a higher mortality rate than males (Policansky 1987).

The intention of this study was to measure the photosynthetic capacity of both a male and a female ramet of the same genotype to better understand the correlation between photosynthetic rates and gender. I hypothesized that females would have a higher photosynthetic capacity than males of the same genotype because of their potentially greater cost of reproduction. Therefore, I measured full light curves of cloned male and female ramets that had been grown under common garden conditions. Photosynthetic measurements were conducted during flowering when the reproductive costs of the inflorescence were likely to have already been met from stored resources, and males and females were most likely to have similar carbon allocation patterns. At flowering, both males and females are supporting reproductive tissue, and, in females, embryos are not yet providing sinks for photosynthate. As both sink strength and whole-plant carbon acquisition are dependent upon organ size, both leaf size and the diameter of the pseudostem were recorded for each individual included in the study.

MATERIALS AND METHODS

Study species. *Arisaema triphyllum*, like other members of the Araceae, is a self-incompatible, diphasic species (Treiber 1980). The dynamics of the gender changing system have been well-characterized (Bierzychudek 1984; Lovett Doust and Cavers 1982; Policansky 1987), and it has been established that plants are vegetative when small, female when large, and male when intermediate in size. A single genetic individual is capable of expressing either gender or of remaining vegetative. The size and reproductive status of any given individual probably reflects resources obtained in the year prior to expression, and is a manifestation of net carbon gain during the previous year (Vitt 1997). Females generally elaborate two leaves and one inflorescence early in the growing season, while males generally produce only one leaf and a single inflorescence. For the duration of the flowering period, carbon gained from photosynthesis may be allocated to tissue maintenance, developing embryos, or the storage organ. Developing embryos and corms are carbon sinks in females, while only corms act as sinks in males.

Common garden. One hundred newly emerging plants were collected from a very large natural population in Chaplin, Con-

necticut, in May of 1992. Asexual reproduction in this species occurs such that vegetative offshoots are quite closely situated to the parent plant, resulting in usually well-delineated groups of shoots. Only individuals that were a minimum of 3 meters apart were collected to increase the probability of including genetically distinct individuals. Plants were grown in the greenhouse for one year, in 6-inch ceramic pots with an equal mixture of sand, peat, and sterilized loam. The pots were placed on greenhouse tables in random order and were rotated every two weeks. A 75% shade cloth structure was erected above the table to simulate forest understory conditions. Pots were watered once a day, and were fertilized once in the growing season with a weak fertilizer solution. Following leaf senescence, pots were moved into a cold room until the following spring.

Eighty-four plants (genets) were chosen at random from the greenhouse population to be planted in an outdoor common garden plot in May of 1993 at the University of Connecticut Plant Research Station in Mansfield, Connecticut. Each plant was placed randomly in a 30 × 30 cm grid so that each individual was 30 cm from the nearest individuals. Plants were then watered and mulched with 2 inches of cocoa hulls, which are relatively inert. The plants were watered only three more times during that summer, and then only during extended periods of no rain. They were not fertilized. The plot was weeded by hand as necessary to eliminate competitors. In early June of 1993, and in June of each subsequent year through 1995, a shade structure consisting of a double thickness of 50% shade cloth was erected over the entire plot to simulate canopy closure at approximately the time during which it occurred in the natural populations. The shade cloth was removed in November of each year. Gender for 1993 was already established at the time of transplant (Vitt 1997), and all but one of the reproductive individuals were female.

Photosynthetic and morphological measurements. Natural production of clones was exploited to produce genets represented by a male, female, and vegetative ramet. Following a two-year period, however, only seven genets included both a male and a female ramet, and only two of these also had vegetative ramets. The majority of newly cloned ramets expressed gender as male because they were smaller than the parent plant. Light curves for all 7 genotypes with a male and female ramet (a total of 14

individuals) were measured using an LI-6200 portable gas exchange system (LiCor Instruments, Lincoln, NE). All measurements were taken during the first two weeks in June while the plants were flowering. The spring of 1995 was slightly late, and in addition, the common garden was situated on a fairly exposed location. Flowering in the common garden, therefore, was somewhat later than in natural populations.

Two or three light curves were measured per day from 0700 to 1400 hours EST to decrease any time effects. Plants were used for measurement only when the leaves were fully expanded, and the inflorescence was considered to be functional. For males, this required that the anthers were either white or pink in color and were actively shedding pollen. Females were considered functional when the ovaries were green, round in shape, and not swollen. The stigmas had to be white and somewhat glossy in appearance. The plant measured at any given time during the day was chosen arbitrarily from those considered functional to ensure that neither males nor females were measured more often at a particular time of day, nor on a particular day in the sequence of days.

A portion of a single leaflet was enclosed in the Lucite leaf chamber, and measurements for each light level began when the CO₂ level in the chamber had reached 360 ppm, which was approximately the ambient CO₂ level in the plot at noon on a sunny day. A fan in the leaf chamber assisted in regulating leaf temperature, and both leaf temperature and humidity were monitored to ensure relative stability during the course of measurements. Leaf area was estimated by tracing the shape of the leaf in the chamber onto graph paper, cutting the shape out, weighing the sample, and converting the weight to area using a previously established weight:area ratio for the same paper. Light levels were controlled by means of screens placed between an artificial light source and the leaf chamber. A heat-reflective glass screen was also used between the light source and the chamber to avoid heat build-up in the chamber.

Leaflet length, leaflet width, and the basal circumference of the aerial shoot (the pseudostem diameter) were measured for each ramet in mid-June of 1995 following full leaf expansion. The relationship between photosynthetic rate and reproductive effort could not be investigated because only one female ramet produced mature fruits in 1995.

Data analysis. The light compensation point, apparent quantum yield, dark respiration rate, and light-saturated photosynthetic rate ($A_{\max}$) for each individual were estimated by fitting a Michaelis-Menten equation (with dark respiration as the y intercept) to the raw data using Proc NLIN (SAS Institute, Cary, NC). These estimates were then analyzed for mean differences among males and females using the paired t-test procedure in Microsoft Excel. Differences in the fitted estimates of $A_{\max}$, dark respiration, and quantum yield among gender and genotype were analyzed with a two-way Analysis of Variance using Proc GLM (SAS Institute, Cary, NC).

Leaflet length and width were summed to obtain a single measure of leaf size. To ensure that this single linear measurement provided an accurate reflection of leaf size, leaf areas of a subsample of thirty individuals randomly chosen from the common garden population were obtained using a hand-held leaf area meter (LiCor 3000A) and regressed against the sum of the leaf measurements ($R^2 = 0.964$, the regression was significant at the 0.050 level). This regression was used to scale the photosynthetic measurements up from a per area basis to the whole-plant level. Differences between males and females in the whole-plant photosynthetic rate were analyzed using the paired t-test procedure in Microsoft Excel. An Analysis of Covariance on photosynthetic rate with pseudostem diameter as a covariate and gender as a main effect, and regressions investigating the effect of pseudostem diameter on photosynthetic rate were performed using SYSTAT 7.0 for Windows (SPSS, Inc., Chicago, IL).

RESULTS

Paired t-tests suggest that males had a significantly higher light-saturated rate of photosynthesis ($7.32 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ vs. $5.73 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $P = 0.050$) and a substantially higher light compensation point (7.67 vs. 2.26 , $P = 0.003$) than females. Neither dark respiration nor apparent quantum yield differed significantly between genders (Table 1). However, two-way analyses of variance of $A_{\max}$, dark respiration, and quantum yield all revealed significant differences between the genders, as well as significant differences among genotype (Table 2) for all three points on the light curve. Figure 1 clearly shows that the males had a higher overall rate of photosynthesis compared with females. In

Table 1. Results of paired t-tests for differences among males and females of the same genotype. There were six degrees of freedom for each t-test conducted. Means are reported with standard deviations. Light compensation point and quantum yield were estimated by fitting a Michaelis-Menten equation to the raw photosynthetic data for each male and female ramet of all pairs of genotypes using Proc NLIN. The Whole Plant Photosynthetic Rate (WPPR) was calculated by scaling Amax up to the leaf area of each individual plant.

	Males $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	Females $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	t-Test
Amax	7.32 $\pm$ 1.65	5.73 $\pm$ 1.09	t = -2.44 <i>P</i> (T $\leq$ t = 0.050)
Light compensation point	7.67 $\pm$ 1.72	2.26 $\pm$ 2.48	t = -4.65 <i>P</i> (T $\leq$ t = 0.003)
Quantum yield	0.07 $\pm$ 0.00	0.13 $\pm$ 0.10	t = 1.22 <i>P</i> (T $\leq$ t = 0.268)
Dark respiration	0.53 $\pm$ 0.22	0.31 $\pm$ 0.32	t = -1.33 <i>P</i> (T $\leq$ t = 0.233)
WPPR	1791.71 $\pm$ 204.13	3421.44 $\pm$ 352.86	t = 3.15 <i>P</i> (T $\leq$ t = 0.010)

Table 2. Results of two-way Analyses of Variance for differences among gender and genotype. Quantum yield estimated by fitting a Michaelis-Menten equation to the raw photosynthetic data for each individual measured using Proc NLIN.

	Model R ²	Source of Variation	df	MS	F	P
Amax	0.794	Genotype	7	23.605	37.53	0.0001
		Gender	1	82.115	130.55	0.0001
Quantum yield	0.516	Genotype	7	0.034	13.28	0.0001
		Gender	1	0.065	25.33	0.0001
Dark respiration	0.477	Genotype	7	0.367	9.24	0.0001
		Gender	1	1.552	39.06	0.0001

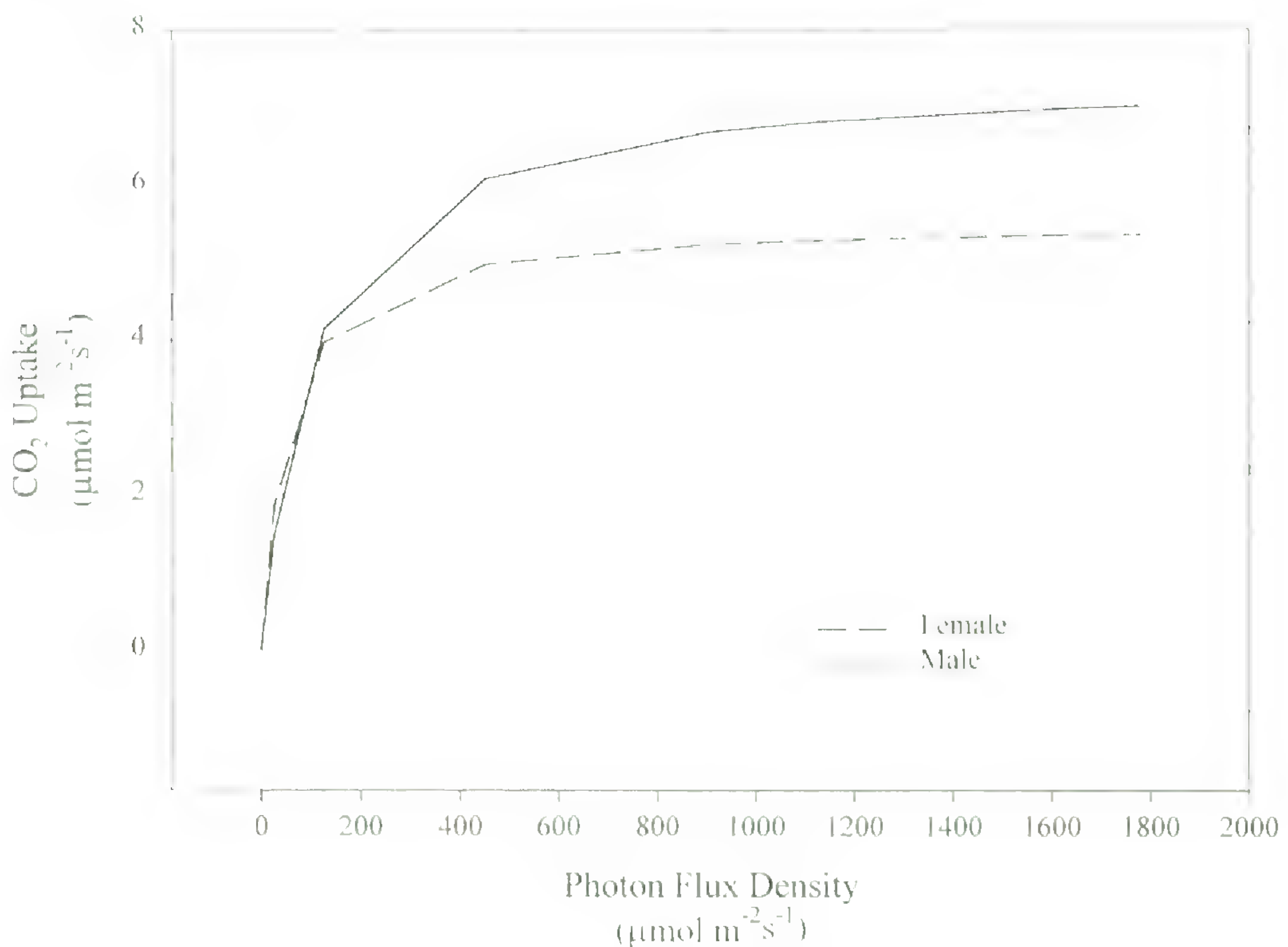


Figure 1. Photosynthetic light response curves averaged across all males (solid line) and all females (dotted line). Values for the curve were obtained by calculating the averages for the maximum rate, A_{max} , light compensation point, apparent quantum yield, and dark respiration.

one pair of clones, however, the female had a higher photosynthetic rate than the male of the same genotype. This female did not fruit. Gender and genotype together describe 79.4% of the variation in A_{max} and 51.6% of the variation in quantum yield, but only 47.7% of the variation in dark respiration.

At the whole-plant level, females had a significantly greater carbon gain than did males, in spite of a lower maximum rate of photosynthesis on a per unit area basis because of their much greater leaf area (Table 2). Total leaf area of males included in the study was $249.26 \text{ cm}^2 \pm 78.2$, while the total leaf area of females included in the study was $611.11 \text{ cm}^2 \pm 189.606$ (means reported with standard deviations). A regression between photosynthetic rate per unit area and pseudostem diameter for females only revealed a significant inverse relationship (Figure 2). Overall, the effect of gender on photosynthetic rate per unit area was no longer evident after controlling for pseudostem diameter (Table 3).

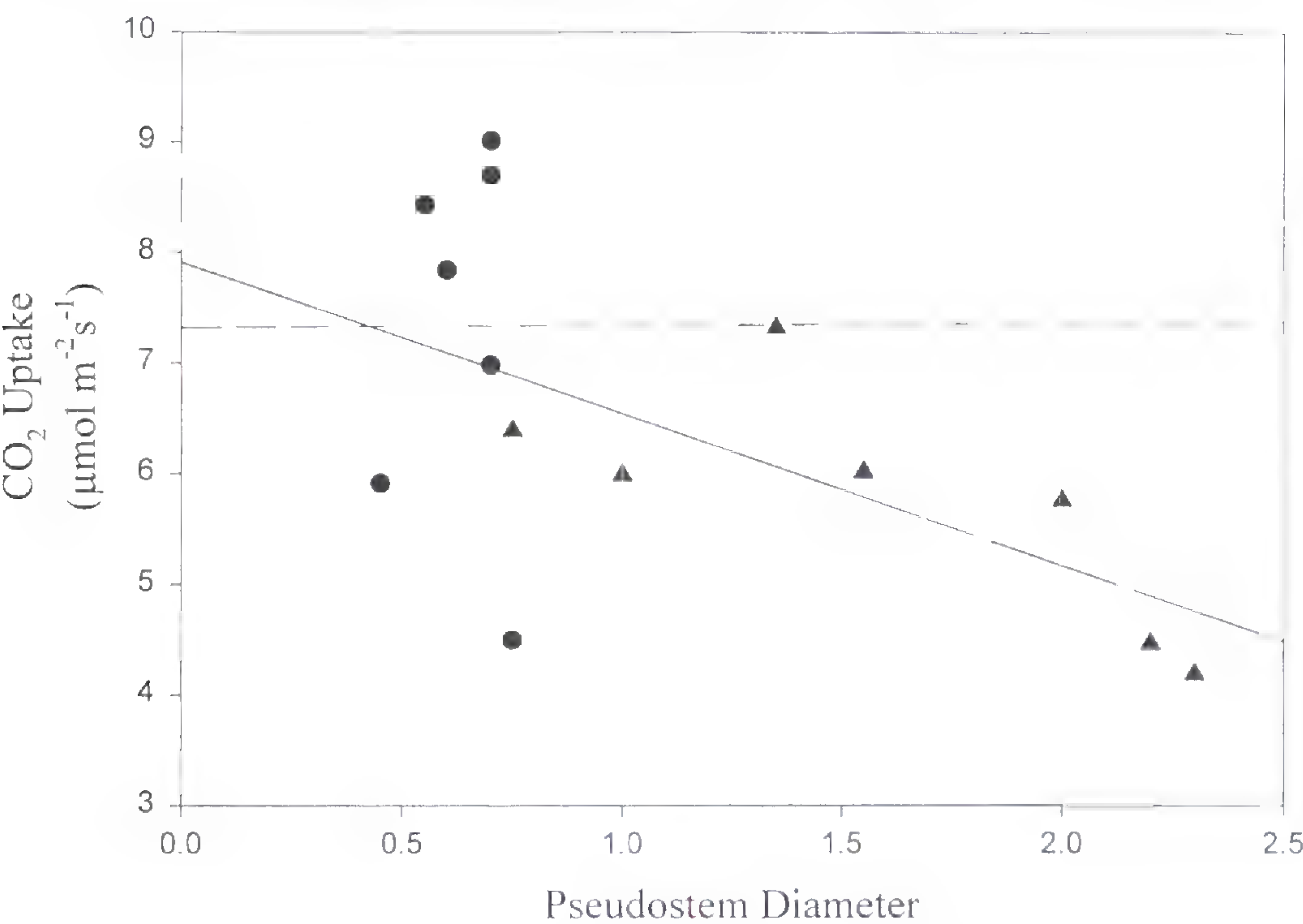


Figure 2. Regressions of photosynthetic rate (CO₂ uptake) and pseudostem diameter (cm). Males: $y = 7.326 + 0.020x$ ($F_{1,6} = 0.0$; $P = 0.998$; $N = 7$; $R^2 = 0.0$). Data points for males are shown as solid circles and the regression line is dashed. Females: $y = 7.913 + -1.368x$ ($F_{1,6} = 6.641$; $P = 0.05$; $N = 7$; $R^2 = 0.570$). Data points for females are shown as solid triangles and the regression line is solid.

Table 3. Results from the Analysis of Covariance with photosynthetic rate as the response variable, gender as a main effect and pseudostem diameter as a covariate. Adjusted Least Squares (LS) means for female and male photosynthetic rates also reported; these represent the photosynthetic rate when adjusted by the covariate.

Source of Variation	SS	df	MS	F	P
Gender	0.162	1	0.162	0.091	0.768
Pseudostem diameter	3.908	1	3.908	2.207	0.166
Error	19.484	11	1.771		
Adjusted LS					
	Mean	SE	N		
Female	6.368	0.660	7		
Male	6.704	0.660	7		

DISCUSSION

Bateman's principle suggests that female reproductive success is limited by resources while male reproductive success is limited by mate availability (Bateman 1948). As a result, males and females are expected to have different patterns of reproductive allocation, with female reproduction incurring greater costs. Many morphological, physiological, and life history traits appear to have become divergent among the sexes of dioecious species in response to differential reproductive costs. It has been suggested that females of dioecious species might have higher photosynthetic rates relative to males of the same species (reviewed in Dawson and Geber 1999; Delph 1999) as differences in the assimilation rates of males and females may arise as a result of increased sink strength in females, driven by maturing embryos and fruits (Dawson and Bliss 1989; Delph 1999; Delph and Meagher 1995).

Arisaema triphyllum has many traits in common with dioecious species for which females are known to have higher reproductive costs relative to males. In particular, larger females produce more flowers, fruits, and seeds than smaller females (Lovett Doust et al. 1986); females devote a greater portion of dry weight to reproductive structures than do males (Lovett Doust and Cavers 1982); and females have a higher mortality rate than males (Policansky 1987). Therefore it was reasonable to hypothesize that females in this species would have a greater photosynthetic capacity than males. However, the results presented above differ significantly from the general expectation that females will exhibit a higher maximum rate of photosynthesis than males (Dawson and Bliss 1989; Dawson and Ehleringer 1993). Males of *A. triphyllum* had significantly higher photosynthetic rates than females of the same genotypes on a per unit area basis.

These results are consistent with other recent studies in which males had higher rates of photosynthesis than females (Gehring and Monson 1994; Laporte and Delph 1996; Marshall et al. 1993; Nicotra 1997). Marshall et al. (1993) have suggested that the sheer number of gametes produced by males may offset the apparent higher cost of female gametes, thus giving rise to a higher overall cost for males. This might then lead to selection for higher photosynthetic rates among males. In *Arisaema triphyllum* photosynthetic rates in males were not correlated with corm size

(measured as pseudostem diameter), therefore it seems likely that current demands for resources may be a sink for males. This raises the possibility that males may have higher reproductive costs than previously expected, and that the higher photosynthetic rates are a response to these demands. It must be pointed out, however, that total carbon acquisition by females far exceeded that of males.

Gehring and Monson (1994) have suggested that leaf nitrogen levels play an important role in determining rates of photosynthesis. In their study, males had higher leaf nitrogen levels than the females, as well as higher photosynthetic rates. They conjectured that females translocate leaf nitrogen to the developing fruits, thereby limiting local photosynthetic rates in the leaves. Nicotra (1997) reported similar results; males in the dioecious species *Siparuna grandiflora* Perkins had higher leaf nitrogen levels, and exhibited higher photosynthetic rates than females that were maturing fruits. In contrast, males of *Phoradendron juniperinum* had higher photosynthetic rates, but there were no differences in leaf nitrogen levels (Marshall et al. 1993). Overall, these findings raise the question: how do females meet the estimated two-fold increase in resource demand for reproduction when they have lower photosynthetic rates? In *Arisaema triphyllum*, greater female size is most likely a response to the greater overall carbon demand that must be met, but at reduced photosynthetic rates. This is consistent with the current finding that as female size increases, photosynthetic rates decrease, and also with the estimates of whole-plant carbon gains that are so much greater for females, as a result of their greater size relative to males of the same genotype.

As the growing season progresses, and carbon demands from maturing embryos and developing fruits increase, the relative photosynthetic rates of males and females may be quite different. Measuring photosynthetic rates throughout the growing season would no doubt yield interesting evidence regarding differential carbon acquisition and allocation patterns among males and females of this species. For example, Nicotra (1997) found that during flowering, females had greater photosynthetic rates, while males exhibited higher rates later during fruit maturation. Although in *Silene latifolia*, males had consistently higher photosynthetic rates than females, while females maturing fruits had

higher rates than females without fruits (LaPorte and Delph 1996).

Genetic differentiation in photosynthetic capacity has been shown between populations (Teramura and Strain 1979; Winn and Evans 1991) and among genotypes (Kuiper and Smid 1985), as well as among family lines (Geber and Dawson 1990). For the individuals studied here it appears that sexual dimorphism in this trait may be influenced by genotype. Average differences among the sexes of dioecious species may mask substantial variation at the individual level. It is possible for the average difference between males and females to be statistically significant (Figure 1), while individual pairs show underlying variation at the same time (Table 2). Thus, the average performance of males and females in a population sample may depend strongly on how representative the individuals chosen for study are of the population as a whole.

Photosynthetic rates in this experiment were measured at or just after flowering to measure carbon acquisition when males and females were supporting similar loads of reproductive tissue (i.e., pedicels, inflorescences, and the bracteolate spathe characteristic of this family). Recent investigations into another aspect of this species' biology, notably the timing of developmental events critical to reproduction, have shown that in addition to maturing and maintaining the current year's reproductive tissues, individuals were also initiating reproductive structures for the next year (Vitt 1997). In effect, plants were assessing, and presumably responding to, both their current and future costs of reproduction simultaneously.

Males in this species senesce earlier in the season than females (Vitt 1997), and it may be that higher rates of photosynthesis have evolved concurrent with the male phase to compensate for the shorter period of carbon assimilation. The underlying mechanism remains a mystery, however there are at least two possibilities. First, as Gehring and Monson (1994) have noted, females may translocate nitrogen to developing seeds, leaving males with a higher leaf nitrogen content allowing them higher photosynthetic rates. In this study, however, photosynthetic measurements were taken at the time of flowering in an effort to control for embryo sink strength. A second possibility is that males may be translocating photosynthate to the corm at a rate exceeding that of females.

The corm is a sink for photosynthate, providing storage for carbon that is assimilated over and above current reproductive and maintenance costs. Corm weight has been significantly correlated with pseudostem diameter ($R^2 = 0.998$, $P = 0.004$; Vitt 1997). Because of the close association of the corm and the pseudostem, physically as well as statistically, pseudostem diameter is a good measure of a plant's current resource status and has been found to be the best overall predictor of current gender (Vitt 1997). Individuals with a smaller pseudostem diameter were male, and the probability of expressing as a female increased with increasing pseudostem diameter.

A regression that included only females revealed a significant inverse relationship between pseudostem diameter and photosynthetic rate; as corm size increased, the photosynthetic rate decreased (Figure 2). There was no relationship between these traits for the males included in this study. While there was some variation in photosynthetic rate among males, there was very little variation in pseudostem diameter, while females had a large variation in pseudostem diameter (Figure 2). The evidence suggests the corm is not as strong a sink for very large females, which have greater stored resources, at least during the flowering phase of the growing season. This conclusion is supported by the Analysis of Covariance reported in Table 3, which shows that the effect of gender on photosynthetic rate is greatly reduced after controlling for pseudostem diameter, and is not significant at the 0.09 level. It must be noted, however, that size and sex expression are tightly correlated in this species making it difficult to determine the separate effects of these variables.

Corm size, and thus sink strength, was affecting leaf-level photosynthetic rates, at least in females. This is consistent with the findings of Laporte and Delph (1996), who found similar patterns in leaf-level photosynthetic capacity. Photosynthetic rates in *Arisaema triphyllum* appeared to be sink-limited in females at the time of flowering, while this did not appear to be the case for males. Males in *A. triphyllum*, despite their lower whole-plant assimilation rate, appeared to use the net carbon gain to change gender in the next growing season. Males had a greater probability of becoming female in the subsequent growing season than females had of remaining female (Vitt 1997). Overall, males and females appeared to have different patterns of carbon assimilation, at least very early in the growing season.

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GROWTH DYNAMICS AND THE TAXONOMIC STATUS OF *CLADONIA LEPORINA*

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ABSTRACT. The unusual gross morphology of *Cladonia leporina* provided the basis for early lichenologists to classify it separately from other species with red apothecia. Their hesitation to include *C. leporina* with other red-fruited species was based on its ascyphose, abundantly branched thallus, which did not match the characteristic cup-shaped morphology of species that were known in the early nineteenth century. *Cladonia leporina* was compared by its author with *C. rangiferina*, which was later recognized within the genus *Cladina*. The concept of a group to accommodate all of the red-fruited taxa in *Cladonia* arose during the nineteenth century. Its morphological parameters were subsequently broadened to include both branched and unbranched species. Contemporary lichenologists have classified *C. leporina* within section *Cocciferae*, in which all of the *Cladonia* species with red apothecia are recognized regardless of morphology. Similar to other branched species with red apothecia, the morphology and morphogenesis of *C. leporina* suggest that this species is allied with taxa outside of section *Cocciferae*.

Key Words: *Cladonia*, Cladoniaceae, lichen morphogenesis, meristems, taxonomic history

Cladonia leporina Fr. is a locally abundant, endemic lichen in the southeastern United States (Florida to New Jersey) and Cuba. In most modern treatments (Ahti 2000; Evans 1947, 1952; Thomson 1967;) it has been placed within *Cladonia* section *Cocciferae* (Delise) A. Evans on the basis of its red apothecia. In addition to red apothecia (attributable to the presence of rhodocladonic acid), the species that are classified within sect. *Cocciferae* generally possess a persistent primary thallus (basal squamules) and unbranched, cup-forming (scyphose) podetia. However, these characters are lacking in *C. leporina*. As early as the nineteenth century, lichenologists suspected that the highly branched, ascyphose podetium and evanescent primary squamules of *C. leporina* suggested affinities with species outside of sect. *Cocciferae*, possibly outside of *Cladonia* Browne *sensu stricto*. However, most later treatments overlooked the morphological anomalies of *C. leporina* and included it within sect. *Cocciferae* solely on the

basis of apothecial color. At present, sect. *Cocciferae* contains species with a wide range of morphologies that have not been sufficiently documented. The primary objective of this paper is to describe the morphogenesis of the fungal meristem in *C. leporina*. Meristem studies in *Cladonia* are relatively new (see Hammer 2000, 2001a), but they provide insights into patterns of variation and variability in this difficult group of lichen fungi. A second objective is to trace the early taxonomic history of *C. leporina*, with a focus on taxonomic applications that represent conceptual shifts in the approach toward this and other lichen species. The goal is to improve the currently accepted taxonomy in *Cladonia* by presenting biologically relevant information based on morphology and morphogenesis of the fungal meristem. While the micromorphology of this species was not considered by earlier workers, their hesitation to include it within section *Cocciferae* seems to have been an appropriate decision.

MATERIALS AND METHODS

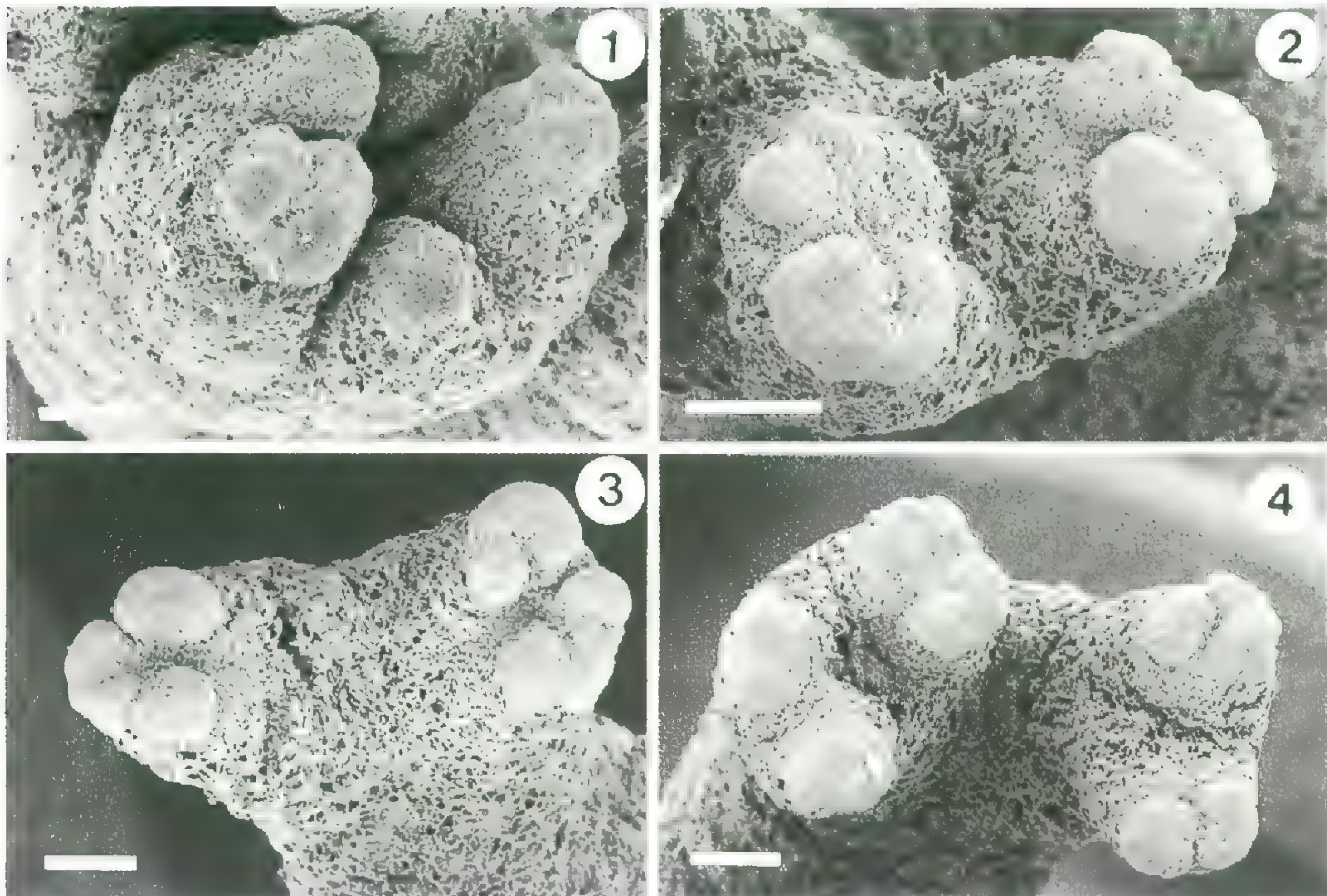
Immature (mostly non-apothecial) specimens of *Cladonia leporina* were studied under the dissecting microscope and were later prepared for scanning electron microscopy (SEM) as described in Hammer (1995, 1996). Scanning electron microscopy was performed at the National Museum of Natural History (Smithsonian Institution) on a Phillips 501 electron microscope at 10–20 kv. Table 1 provides a list of selected specimens studied. A note on the terminology used in this paper seems appropriate. The term “meristem,” which is usually applied to plants (see Barlow 1989) is used in a broad sense in this paper (see Hammer 2000, 2001a). It refers to the purely fungal tissue system that is usually (but not exclusively) found near the apices of *Cladonia* lichens. It is called a meristem because it gives rise to the rest of the hyphal cells of the podetium (see Hammer 1993). Similarly, the term “branch” is most appropriately applied to plant form (see Bell 1991). It has also been used to describe lichen growth, particularly the narrow, elongate structures that arise laterally or apically from the erect, secondary thallus (podetium) in *Cladonia* (see Hammer 1997b).

Table 1. Representative specimens of *Cladonia leporina* examined for this study.

Specimen	Locality
<i>Tucker 10118</i> (FH)	Alabama
<i>Evans 650</i> (FH)	Florida
<i>Hammer 7733</i> (FH)	Florida
<i>Hammer 7750</i> (FH)	Florida
<i>Rapp 15</i> (FH)	Florida
<i>Thaxter 158</i> (FH)	Florida
<i>Small s.n.</i> (coll. 1894) (FH)	Georgia
<i>Seymour & Earle 9195</i> (FH)	Mississippi
<i>Evans 214</i> (FH)	North Carolina
<i>Ravanel s.n.</i> (FH)	South Carolina
<i>Parks 21259</i> (FH)	Texas
<i>Luttrell 1904</i> (FH)	Virginia
<i>Imshaug 25324</i> (FH)	CUBA
<i>Wright s.n.</i> (FH-TUCK)	CUBA

RESULTS

The podetia of *Cladonia leporina* are abundantly branched, but in general the branches are initiated closer to the base than in species such as *C. furcata* (Huds.) Schrad. or *C. crispata* (Ach.) Flot. Further, the branches of *C. leporina* lack the axial openings that characterize most other branched species in the Cladoniaceae. Branching in *C. leporina* can be traced to the ontogeny of the fungal apical meristem. In particular, the initial patterns of meristem splitting are reflected in later branching morphology. The meristem, which initiates and controls growth in *C. leporina*, splits early and frequently during ontogeny. The indeterminate number of branches at maturity and their varied orientation reflects early variations in filial meristems. The asynchronous development of separate meristems and torsion of the axis of growth leads to further variability at maturity. Meristem splitting and subsequent branching of the lichenized thallus is dichotomous but not necessarily equal (Figures 1–4). After the meristem splits, certain bundles develop faster than their filials, enlarging and splitting before same-age bundles have developed apace (see meristems labelled c and c' in Figure 5). In general, the meristem splits dichotomously. However, the angle of divergence varies among filial meristems and this tends to increase during ontogeny. For example, the initial meristem splits occur at relatively small



Figures 1–4. Early ontogeny of *Cladonia leporina* (SEM). 1. Dichotomous branching with limited meristem splitting. The left-hand branch system (two meristems) shows an enlarging meristem below. 2. Two developing branch systems from an initial split (arrow). Right-hand branch system (three meristems) is further developed than the left-hand branch system, which is incompletely split into two bundles. 3. Two well developed branch systems separated by lichenized tissue (note loose network of surface hyphae). 4. Advanced meristem growth with several meristems on two branches. Note that the meristems have split at various angles. All scale bars = 100 μm .

angles (Figures 1, 5), which increase during later growth (Figures 4, 5). As a result, the axis along which splitting occurs and the orientation of filial bundles differ. In addition, torsion of the meristem occurs, leading to variable branch orientation later in ontogeny (Figures 2–4). Further, a group of more or less same-age branches may develop at various rates, resulting in the apparent deformation of a roughly circular or ovoid grouping of meristem bundles (Figures 6–9). The development of a roughly ovoid apical cluster is often accompanied by the exaggerated development of lichenized tissue below. In general, the meristems split and develop slowly, while the tissue beneath them develops relatively quickly. The result is an urn-like podetial shape that is narrow at the apex and wider below (Figure 6). The meristem eventually separates during ontogeny as the branches become longer (Figure 7), but the process of separating may be delayed so that branching

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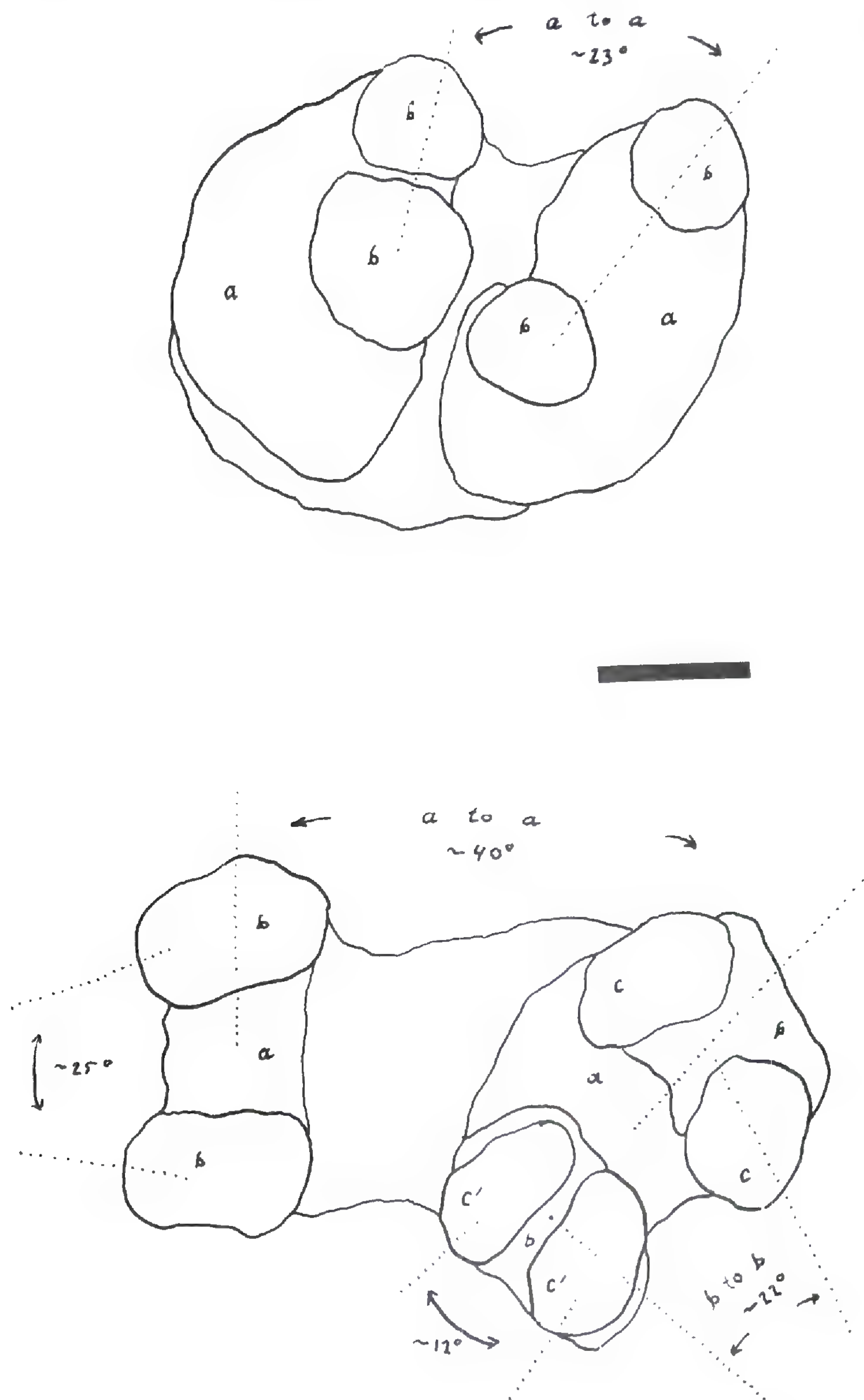
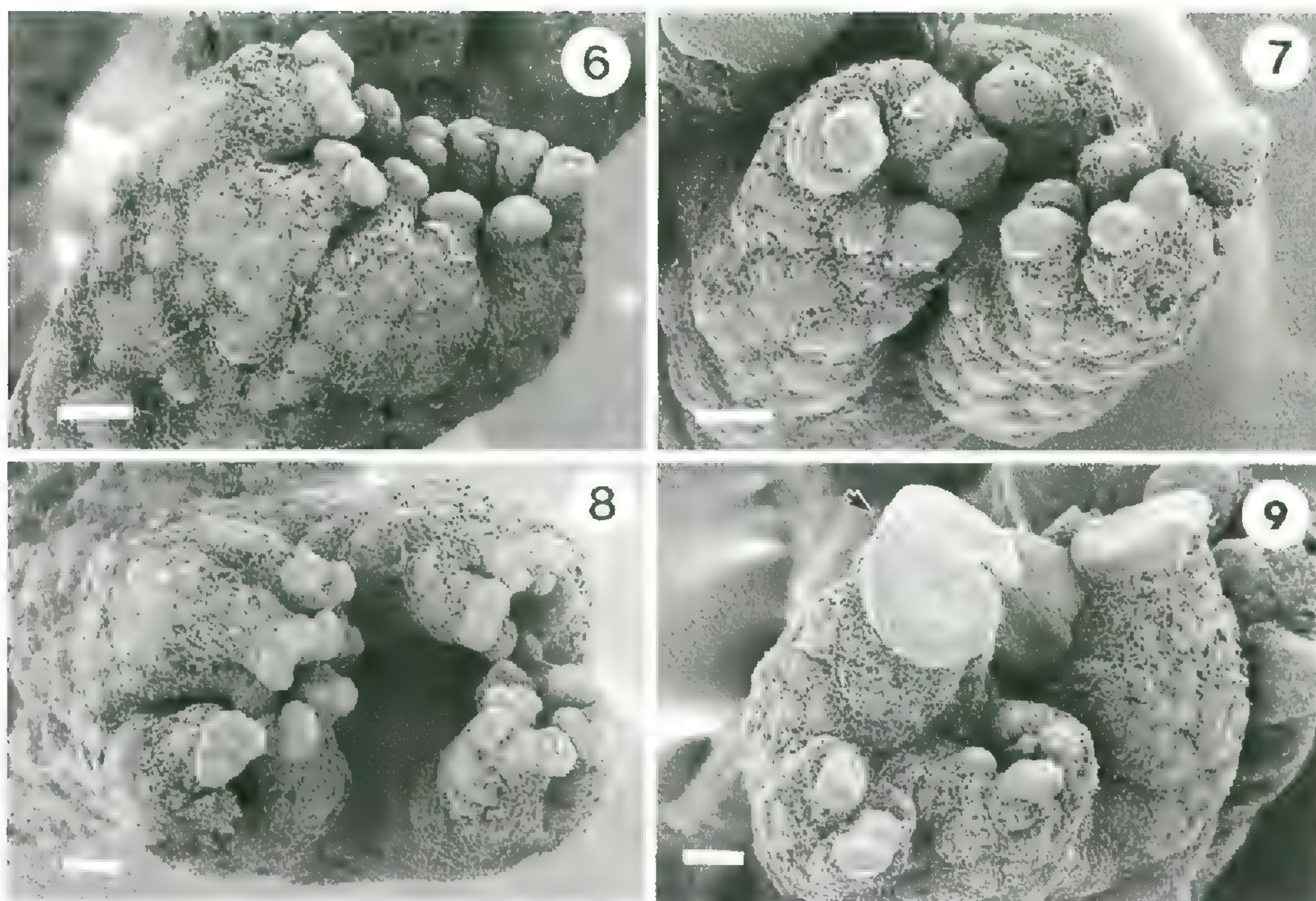


Figure 5. Diagrams based on SEM photographs of *Cladonia leporina* illustrating approximate angles of meristem divergence among filials. Note that the angle of divergence increases between older meristem filials. ("a" indicates oldest filials). Scale bar ca. 100 μ m.



Figures 6–9. Later meristem development in *Cladonia leporina*. 6. Portion of developing podetial apex. Meristems have split but remain clustered around a central axis. 7. Later apical development with more or less same-age (filial) branches with meristems at various stages of development. 8. Further meristem splitting at podetial apex. Note underlying axis (lichen tissue) and thick bases of developing branches. 9. Developing apothecium (arrow) adjacent to immature branches that are tipped by meristem tissue (below). All scale bars = 100 μm .

in certain parts of mature podetia is indistinct (Figure 8), especially when observed macroscopically. In some podetia, the difference in rates of meristem development is highly pronounced, and apothecia may develop on branches that are roughly the same age as branches that are tipped by the immature meristem (Figure 9).

DISCUSSION

The branching ontogeny of *Cladonia leporina* occurs through various processes. Enlarging and splitting meristems are the major factors that influence morphogenesis of the branched lichenized podetium, but other factors control the development of branches as well. For example, torsion and synchronization influence the outcome of form in *C. leporina*. In addition, the growth and development of lichenized tissue immediately below the

branches affects branching patterns and morphogenesis in this species, similar to the pattern seen in the Australasian endemic *C. pertriosa* Kremp. (see Hammer 2001b). *Cladonia leporina* is characterized by branching, but cup-like or urn-like growths are also present in this species. However, the development of cups does not occur as described in Hammer (1993, 2000). Instead of the cup forming from a single meristem that undergoes various growth processes, the cup-like form of *C. leporina* is a by-product of relatively slow meristem splitting accompanied by the growth of more massive supporting lichenized tissue. The cup-like shape may be maintained by the mechanical force of the tissue beneath the meristem, in contrast to other species in which the shape of the cup is determined by the outward growth of a single toroidal (donut-shaped) meristem. Thus, the cup of *C. leporina* is the product of a developmental pathway that is distinct from other *Cladonia* species. The cup in *C. leporina* is analogous, not homologous to cups in other *Cladonia* species. Thus *C. leporina*, as described by early workers, is ascyphose when the morphogenesis of its cups is compared to that of other *Cladonia* species.

Historically, the unusual morphology of *Cladonia leporina* was considered more important than its apothecial color in the taxonomic placement of the species. When the species was first described by Fries (1831), it was not classified among red-fruited taxa, in which all the known species possessed cups. Fries was equivocal about the placement of *C. leporina* and he compared its morphology to *Cladonia* (= *Cladina*) *rangiferina* (L.) Nyl., a branched species with brown apothecia. However, Fries stressed the red apothecia (“apotheciis coccineis distinctissima”) of *C. leporina* and he understood that they required some sort of taxonomic distinction. Fries sought a solution to the problem of *C. leporina* within another morphological parameter based on the characteristics of the primary thallus. His taxonomic system recognized two sections in *Cladonia* based upon the primary thallus and its morphology. Section I was characterized by a leaf-like (squamulose) primary thallus. He included four series within this section based on apothecial color. However, he did not place *C. leporina* within the so-called Series IV (*Cocciferae*), with the other red-fruited species. Rather, he placed *C. leporina* in an ambiguous position between his species number 210 (*C. macilenta* Hoffm.), which was the last species in Section I, and species number 211 (*C. rangiferina*), the first of three species in Section

II, which was characterized by a crustose primary thallus. Fries added to the ambiguous position of *C. leporina* by including its description in the paragraph that introduced Section II, but he did not assign it a species number!

The diagnosis of *Cladonia leporina*—"Thallus horizontalis crustaceo-granulosa, granulis in podetia abeuntibus. Podetia uniformia, fruticulosa, ascypha, definite ramosa"—was included in Fries' description of his Section II, which he referred to the group *Pycnothele* of Acharius (1803). The three species in Section II, *C. rangiferina*, *C. uncialis* (L.) Wiggers, and *C. papillaria* (= *Pycnothelia papillaria* Dufour) were placed together on the basis of their crustose primary thallus. Thus in the case of *C. leporina*, Fries followed the tradition that was begun by Acharius, who classified the species by morphology instead of apothecial color. Flörke (1828) had also followed this tradition. For example, three years before *C. leporina* was described, he placed the red-fruited *C. incrassata* Flörke in the group *Clavatae* with species of similar morphologies and various apothecial colors. While Acharius, Flörke, and Fries did not ignore the color of the apothecium, it did not take precedence over morphology in their systems.

By contrast, Delise (in Duby 1830) used color as a major taxonomic character. He erected the *Cocciferae* grouping within the genus *Cenomyce* (= *Cladonia*) to accommodate all of the species with red apothecia together, irrespective of morphology. Nylander (1858) adopted Delise's approach, with a stress on color as the deciding factor in the classification of many of the species of *Cladonia*. Tuckerman (1882) also based his classification of *Cladonia* upon the color of the apothecia. However, he struggled to accommodate the unusual morphology of *C. leporina* within his system. Tuckerman recognized three series in *Cladonia*. He included *C. leporina* as the last species (number 31) in Series III (*Coccineae*) taking care to compare its morphology to brown-fruited species in Series I (*Fuscae*). By referring to the group *Fuscae*, Tuckerman compared *C. leporina* to varieties of the branched species *C. furcata*, including var. *crispata* (= *C. crispata*). Tuckerman also mentioned the similarity between *C. leporina* and *C. rangiferina* that Fries had observed. The monographer Vainio (1887) listed *C. leporina* as the last species (his number 36) in the *Cocciferae*, following *C. cristatella* Tuck. In Vainio's taxonomy (it is noteworthy that he considered it to be a phylogenetic arrangement), the species that followed *C. leporina*

was the brown-fruited *C. aggregata* [= *Cladia aggregata* (Sw.) Nyl.]. Like Fries, Vainio held an equivocal view of the placement of *C. leporina*. He described it as “ascypha,” which reflects the gross morphology of the highly branched podetium, but he included it marginally within the *Cocciferae*.

Evans (1947, 1952) considered *Cladonia leporina* in several papers. He compared its morphology to species in the genus *Cladina* as well as to *Cladonia uncialis*, a brown-fruited species with characteristically perforate branch axils (largely absent in *C. leporina*). While Evans placed *C. leporina* in the *Cocciferae*, he proposed a new monotypic taxon (series *Leporinae*) to accommodate its morphology (Evans 1938). *Leporinae* was unique in that it was based on morphological characters while the other groupings within *Cocciferae* were based solely upon color differences in the species. Thomson (1967) later included *C. leporina* as the final species in the *Cocciferae* but did not provide a particular heading for it or any of the other red-fruited *Cladonia* species. Ahti (2000) included *C. leporina* as one of 38 (alphabetically arranged) *Cocciferae* species in the neotropics. The group delimited by Ahti shows a very wide range of morphological characters. Many of the species are new to science and require further morphological study.

If *Cladonia leporina* is to be included in sect. *Cocciferae* along with other branched, red-fruited species such as *C. cristatella* (see Hammer 1997c), *C. incrassata* (Hammer 1997a), or the recently described *C. piedadensis* Ahti (see Ahti 2000), then we may assume a very broad range of morphologies within the group, which has traditionally been circumscribed upon the basis of apothecial color alone. Contemporary lichenologists have classified *C. leporina* within sect. *Cocciferae*, in which all of the *Cladonia* species with red apothecia are recognized regardless of morphology. The underlying assumption of this classification system is that taxonomically, chemistry and color are more important than morphology in *Cladonia*. From a phylogenetic standpoint, this would imply that the production of rhodocladonic acid, which results in red apothecia, arose once in *Cladonia* and probably denotes a monophyletic group. Following this assumption, morphological or morphogenetic characters would perforce represent multiple evolutionary events. That certain morphologies arose a number of times is a scenario that is difficult to accept given the apparently tight controls on early morphogenesis in the Cladoniaceae.

(see Hammer 2001a). Further hypotheses about monophyly among *Cladonia* species have yet to be tested, but so few taxa have been analyzed morphologically that pertinent information is still lacking. Preliminary molecular data (see Stenroos and DePriest 1998) support the hypothesis that the species in sect. *Cocciferae* are related, but most of the species in the group have not yet been studied. Perhaps more important, the genetic basis for the production of rhodocladonic acid is unknown. Does it represent an autapomorphy that characterizes sect. *Cocciferae*? Alternatively, might sect. *Cocciferae* be more a product of the cognitive biases of taxonomists than biology? In other words, has the ease with which red apothecia are recognized contributed to the taxonomic decision to classify the red-fruited species together? Most significantly, what are the genetic controls over morphogenesis in *Cladonia* fungi? In order to better evaluate the taxonomy of sect. *Cocciferae* and the Cladoniaceae in general, future projects should undertake to examine the inherited pathways by which form and color are attained. This may help to improve the state of our knowledge concerning the origin and relationships of the Cladoniaceae, which is still quite vague. Until then, two considerations might be applied to the taxonomy of *Cladonia*, with the goal of constructing more biologically relevant groupings within the genus. From a narrow perspective, *C. leporina* should be classified apart from the *Cocciferae*. More broadly, rather than struggle to classify *C. leporina* in a similarly arbitrary grouping, the problems of its taxonomy should serve as a focal point for reconsidering all of the subgeneric taxa in *Cladonia*.

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THE SURVIVAL OF *VAUCHERIA* (VAUCHERIACEAE)
PROPAGULES IN DESICCATED NEW ENGLAND
RIPARIAN SEDIMENTS

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ABSTRACT. Species of the algal genus *Vaucheria* routinely leave “seed banks” of propagules in riparian sediments for regrowth during optimal conditions in the habitat. Muds containing propagules were collected at different times of the year from four freshwater riparian habitats in central and eastern Connecticut, sites previously known to have as many as six *Vaucheria* species living sympatrically in the space of just 36 cm² of floodplain sediment or stream bank. Muds from each site were allowed to thoroughly desiccate in the laboratory. Desiccated mud samples were rehydrated after prescribed periods of time, and then cultured under optimal conditions in an incubator. Eight freshwater species appeared variously in the cultures demonstrating a tolerance to desiccation of 63–383 days with *V. undulata*, *V. prona*, and *V. frigida* surviving the greatest periods of treatment.

Key Words: desiccation tolerance, propagules, riparian sediments, seed banks, *Vaucheria*

Angiosperms—and in particular annuals—often accumulate seeds in soils as viable buried reserves or seed banks for when environmental conditions are optimal for germination (Begon et al. 1996). These seed banks allow flowering plants to survive periods of environmental stress, ensuring a species’ eventual return to a normally suitable habitat. Such is the case when spring rains allow short-lived annuals to reappear in the desert. In wetlands, as water recedes from the margins of lakes, ponds, streams, and wet meadows, these habitats are often rapidly exploited by germinating seeds of grasses and herbaceous annuals that have broken dormancy (Keddy 2000). These are species requiring a greater soil O₂ content for germination than when inundated with water. When Darwin (1859) removed less than a full teacup of mud from the edge of an English pond, 537 seeds germinated in

the next half year after allowing the mud to dry somewhat on his study windowsill. Such “seed banks” are also found among aquatic animals and protists that leave desiccation-resistant fertilized eggs or other propagules in habitats on a seasonal basis or when conditions are unsuitable for continued growth (Begon et al. 1996). In the New England terrestrial habitats where the yellow-green alga *Vaucheria* (Vaucheriaceae, Tribophyceae, Chrysophyta) grows, optimal wet conditions are not permanently sustained, and propagules that have been produced remain in the substrate as the “seed bank” for the next period of active growth after an interval of environmental stress such as desiccation.

Between 40–50 different species of *Vaucheria* have been reported from North America, with approximately three-quarters of these living in freshwater habitats and the remainder in brackish or marine waters (Blum 1972; Brown 1929). These algae are some of the most frequently encountered macroscopic terrestrial algae, dwelling on and in wet soils and muds throughout much of North America. In particular, *Vaucheria* species are common in riparian habitats, along stream and river banks and their associated floodplains. Under optimal conditions, dense, felt-like mats form, at times to 4–6 cm deep (Gallagher and Humm 1981), as populations grow throughout and above the substrate. *Vaucheria* mats frequently appear on the banks of streams and rivers, and it has been speculated that the coenocytic siphons aid in the prevention of bank erosion (Gallagher and Humm 1981; van den Hoek et al. 1995), as demonstrated for other terrestrial algae that bind soils together (Bailey et al. 1973; Cameron and Devaney 1970; Fletcher and Martin 1948). *Vaucheria* is also commonly found in disturbed habitats as a pioneer on newly exposed sediments such as floodplain marsh beds after deposition of new alluvium.

Unlike the periodic desiccation experienced by intertidal seaweeds, freshwater algae in riparian habitats experience periods of flooding and drought that are uncertain in length, making tolerance of water stress all the more crucial (Morison and Sheath 1985). Many studies have examined the germination of angiosperm seeds following periods of extended desiccation, but only a fraction have looked at the survival of freshwater algae in such circumstances. These investigations used air-dried agricultural soils that, when hydrated with nutrient media, ultimately produced cyanobacteria and green algae even after years of desic-

cation (Bristol 1919, 1920; Trainor 1970, 1985; Trainor and Gladych 1995). When examining the viability of terrestrial algae in some English soils, Bristol (1920) made the only report of *Vaucheria* surviving extended desiccation, finding *V. hamata* Vaucher after 45 days without moisture. Although not discussed or directly observed, one could assume the *Vaucheria* that appeared in Bristol's cultures was generated from a "seed bank" of propagules left by the alga during a period of abundant growth to survive periods of desiccation or other environmental stress.

A variety of structures produced by *Vaucheria* both sexually (oogamy) and asexually are encompassed by the term propagule, including the fertilized female oogonium (oospore), terminally "cut-off" vegetative fragments, aplanospores, and synzoospores (Greenwood 1959; Ott 1975; Rieth 1980). During periods of prolonged desiccation, it is possible that the cytoplasm concentrates within the coenocytic siphon and becomes separated by a wall, forming a dormant cyst-like structure commonly found in other groups of algae (Hoffmann 1989). Any of these propagules can be used to re-establish a population of *Vaucheria* when conditions for growth are suitable in the microenvironment. As *Vaucheria* is such a ubiquitous alga in riparian habitats, we have set out to test the ability of several species to tolerate water deprivation, a phenomenon that naturally occurs in the summer in New England floodplains.

STUDY AREAS

Four freshwater Connecticut sites were chosen based on previous collections of many sympatric *Vaucheria* species (Schneider et al. 1999):

1. Burleson's Brook (BUR) — Suffield, Tolland Co., adjacent to Burleson's Brook on Conn. Rt. 187 at the Connecticut-Massachusetts state line (42°02.063'N, 72°41.210'W);
2. Nipmuck Trail (NK) — Ashford, Windham Co., approximately 3 km from an entrance to the Nipmuck Trail, a portion of the Mohawk Trail system, on Conn. Rt. 74 (41°51.301'N, 72°12.821'W);
3. Scantic River (SCR) — Enfield, Tolland Co., floodplain directly beneath the bridge on Conn. Rt. 190 that crosses over

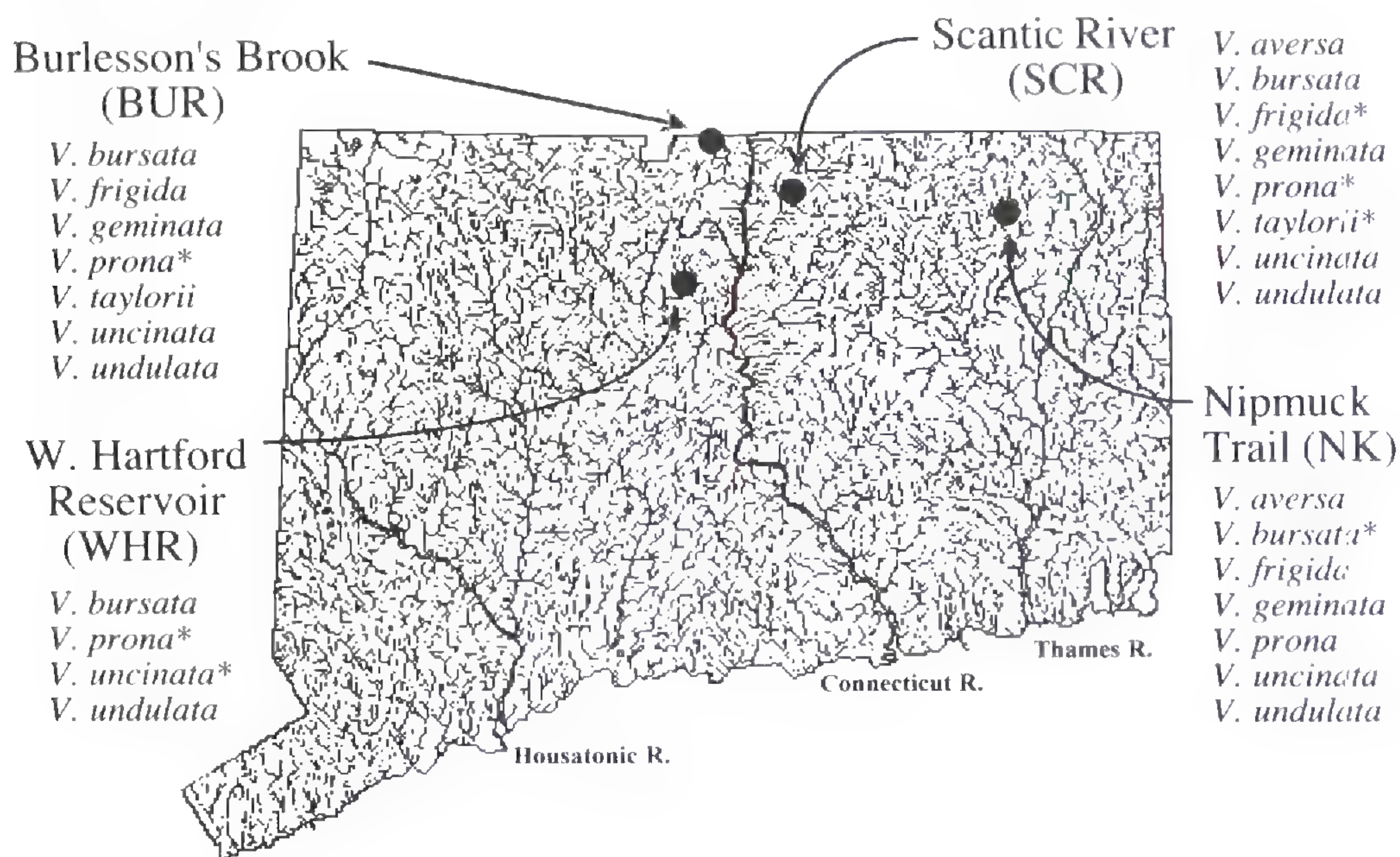


Figure 1. Connecticut, U.S.A. collection sites and their known *Vaucheria* species. Species discovered at each site for the first time are marked with an asterisk (*), the remainder are from Schneider et al. (1999).

the Scantic River near the intersection with Conn. Rt. 191 (41°58.966'N, 72°30.969'W);

4. West Hartford Reservoir (WHR) — West Hartford, Hartford Co., a low valley east of a recreational trail and the slow-moving stream outflowing from Wells Pond west of Conn. Rt. 44 and east of the reservoir (41°47.411'N, 72°47.099'W).

These sites are inhabited by eight of the eleven known freshwater species of *Vaucheria* found in Connecticut: *V. aversa* Hassall, *V. bursata* (O. F. Müll.) C. Agardh, *V. frigida* (Roth) C. Agardh, *V. geminata* (Vaucher) DC., *V. prona* T. A. Chr., *V. undulata* C. C. Jao, *V. uncinata* Kütz., and *V. taylorii* Blum (Figure 1). The remaining three freshwater species, *V. compacta* (Collins) Collins ex W. R. Taylor, *V. lii* Rieth, and *V. racemosa* (Vaucher) DC., have been observed only rarely in Connecticut and were not included in this study (Schneider and Lane 2000; Schneider et al. 1999).

MATERIALS AND METHODS

Longitude and latitude were fixed using a GarminTM GPS 12 (vers. 4.57). At each of the four sites, bulk samples of the top 3–

4 cm of damp/wet mud from several locations were collected, with or without visible *Vaucheria* siphons, using a flat-nosed shovel. Mud was taken during all seasons except winter when substrates were frozen (ix.98, iii.99, vi.99). In the lab, 20–30 ml of water were added to the bulk samples so they could be thoroughly mixed. The mud slurry was then spread evenly to a depth of 1.5–3.0 cm in a 42.5 × 35.0 cm photographic developing tray, and left exposed to desiccate at 23–25°C. After the mud had dried for 3–4 days, it was cut into squares approximately 36 cm². The blocks were then left to dry in the trays until ready for rehydration. Every 5–20 days after partitioning into blocks, desiccated mud samples from each site and collection date were placed in plastic culture dishes (3.5 × 8.5 cm) and rehydrated with Bold's basal medium (Bischoff and Bold 1963), such that approximately 0.5–1.0 cm standing medium remained in the dish after mud saturation. For the purposes of this study, "days desiccated" (Table 1) refers to the amount of time from partitioning of the blocks in the exposed trays to rehydration, although the mud was not completely desiccated for the first week. In order to establish which *Vaucheria* species were present in the mud samples to be desiccated, control cultures of the same size were established from each site and sampling date. The controls were immediately placed into individual culture dishes with Bold's medium.

All culture dishes were incubated in a Hotpack™ growth chamber under a 16L:8D diurnal cycle at 15°C, with cool white fluorescent lights and an irradiance level of 3.49–16.58 μmol/m²/sec, conditions found optimal for the growth of a wide variety of *Vaucheria* species (Schneider et al. 1993, 1999). Cultures were examined for *Vaucheria* siphons using a dissecting microscope every 7–10 days. As siphons appeared, small amounts were removed for examination under a compound microscope to search for gametangia—characteristics used to distinguish species.

RESULTS

Most of the experimental cultures became reproductive, allowing the identification of 4–7 species at every site. *Vaucheria* collected in muds from all four sites was shown to tolerate desiccation for a period of nearly 200 days, with propagules of *V. undulata* from SCR showing the greatest tolerance, surviving 383 days of desiccation (Table 1), followed by *V. prona* (359 days)

Table 1. Desiccation tolerance (in days) of eight *Vaucheria* species in mud collected on several dates from four Connecticut riparian sites. Collection site abbreviations are defined in the text and Figure 1. Brackets indicate that the species appeared in control cultures for the collection at that site. Data for species appearing in experimental dishes that did not appear in the accompanying control dishes are listed without brackets.

Species	No. of Days of Desiccation Tolerated									
	Coll. Site: Coll. Date:	BUR I iii.99	BUR II vi.99	BUR III x.99	NK I ix.98	NK II vii.99	SCR I vi.99	SCR II x.99	WHR I vi.99	WHR II x.99
<i>Vaucheria aversa</i>		—	—	—	[41]	145	[110]	94	—	—
<i>Vaucheria bursata</i>		[—]	[130]	84	—	[91]	119	94	59	—
<i>Vaucheria frigida</i>		[—]	[49]	189	[12]	[49]	320	—	—	—
<i>Vaucheria geminata</i>		—	—	56	—	—	16	144	—	—
<i>Vaucheria prona</i>		—	49	219	22	[59]	[359]	154	[133]	—
<i>Vaucheria taylorii</i>		—	[—]	—	—	—	—	63	—	—
<i>Vaucheria uncinata</i>		—	[118]	30	[18]	[—]	16	—	193	—
<i>Vaucheria undulata</i>		[178]	[198]	219	[229]	[99]	[383]	154	[193]	68
<i>Vaucheria</i> spp.		240	198	219	229	153	383	154	193	72

and *V. frigida* (320 days). *Vaucheria* survived desiccation for 240 days at BUR, 229 days at NK, and 193 days at WHR. Among the species, *V. undulata* again survived the longest treatment in all but one collection at these three sites (Table 1). In the NK II mud sample, *V. aversa* showed the greatest tolerance to desiccation (145 days).

Certain species previously known from a site (Schneider et al. 1999) never appeared in either the control or experimental dishes of the present study: *Vaucheria geminata* at NK and WHR, *V. aversa* at BUR and WHR, and *V. taylorii* from SCR. Presumably, these species had not left a significant "seed bank" in the sediments prior to each of the collections to allow a new population to flourish, as even the controls did not produce them. Conversely, some species were discovered in our cultures that had not previously been found at each site, including *V. prona* from BUR, SCR, and WHR. These species are marked with asterisks (*) in Figure 1. In the present study, 50–80 mud blocks from each site were rehydrated over time, increasing the likelihood that a species might appear due to the greater sample size. The most infrequently discovered species, *V. taylorii*, previously known only at BUR among the four sites, appeared in a BUR II control dish and in SCR II after 63 days of desiccation. Several other species appeared in the desiccated mud blocks of each site and not the control cultures of the same collection (Table 1, number of days not bracketed), or in the controls but not the rehydrates (Table 1, bracketed dashes).

DISCUSSION

The genus *Vaucheria* is widely distributed throughout North America except in areas with prolonged drought such as the southwestern United States. Prescott (1938) suggested that terrestrial species of *Vaucheria* favor habitats where adequate precipitation, humidity, and cold temperatures are found, but the alga can also thrive where average surface temperatures reach as high as 50°C, providing sufficient water content is present in the substrate. Unlike algae with partitioned filaments, *Vaucheria* has the ability to allow unrestricted cytoplasmic flow within a coenocytic siphon, allowing the transport of water, CO₂, and nutrients to portions of the alga which are above the surface of the substrate, and O₂ and photosynthetic products to portions below the mud.

Therefore, although parts of an alga might not have access to optimum conditions for photosynthesis or nutrient/water uptake, *Vaucheria* may still be able to grow optimally due to its exposure to both the substrate and atmospheric environments.

Previous studies of *Vaucheria* have demonstrated a staggered emergence of different species, attributed to competitive interactions with biological and seasonal changes (humidity, temperature, water content in soil) further regulating the development (Nienhuis and Simons 1971; Schneider et al. 1999; Simons 1975). It is possible that higher numbers of propagules are produced and released in the winter and spring when moisture and nutrient contents in the soil are high (Islam 1984). In fact, many species of *Vaucheria* are reported by Blum (1972) to be reproductive only in winter through spring in North America. Nevertheless, in the present study, the time of mud collection seemed to have little effect on the species ultimately appearing in our cultures (Table 1), perhaps due to the abundance of ungerminated propagules in our mud sample “seed banks” whenever collected. Not all of the species in this study produced robust “seed banks”; thus, their survival during desiccation can hardly be considered definitive. *Vaucheria taylorii* appeared in only two of the 261 total dishes from all of the sites, presumably showing its lesser presence in the *Vaucheria* “seed bank.” Whether 63 days of survival is near the high end of success this species can attain is difficult to know based upon its presumed small number of propagules in the collected muds.

We have been able to demonstrate that eight Connecticut species of *Vaucheria* were able to survive extended periods of desiccation in a controlled laboratory experiment. *Vaucheria undulata* tolerated desiccation for 383 days and *V. prona* for 359 days, periods eight times longer than that demonstrated by Bristol (1920) for *V. hamata*. The results we present for each of the species show the survival of *Vaucheria* propagules to a specific environmental stress far beyond what would normally impinge upon species in a temperate, seasonally variable, generally moist New England environment, where such prolonged periods of drought are unlikely to occur under normal circumstances. Given the results presented here, desiccation does not appear to be a limiting factor to the success of *Vaucheria* in a given habitat, providing it has initially established a reproductive population and buried a “seed bank” of propagules.

It is interesting to note that the two *Vaucheria* species that appeared most frequently in our desiccated mud samples, *V. prona* and *V. undulata*, are in fact the most widely distributed and commonly collected species in Connecticut (Schneider et al. 1999). *Vaucheria undulata* was the only species to appear in each of the nine desiccated mud samples (Table 1). In our rehydrated cultures, *V. prona* and *V. undulata* were observed to occur simultaneously with great frequency at each of the four collection sites, and until their reproductive periods had concluded, often with virtually complete exclusion of all other *Vaucheria* species. *Vaucheria uncinata* and *V. bursata* were also found at all four sites (Figure 1). The appearance at different times, and establishment of these species in the mud cultures for varying lengths of time, may indicate that certain species can outcompete others for available nutrients, water, or substrate. However, there is no way to guarantee that propagules of all of the species were evenly spread throughout the original bulk samples from each site, a concern inherent with our experimental procedures. Furthermore, a single mud sample taken at one point during the year may be unable to accurately reflect diversity and abundance of the total algae present at a given site (Hunt et al. 1979), as the "seed bank" is replenished by the varied species actively growing at different times of the year. For example, the desiccated muds from WHR collected in June produced four species of *Vaucheria*, while October samples from the same site produced only one (Table 1). Reproductive periodicity caused by intraspecific or other mechanisms can cause what Hoffmann (1987) described as a temporal and spatial patchiness of "propagule rain." The abundance of a particular species' propagules is therefore dependent upon its seasonal or periodic reproduction. Persistent seed pools in the soil are characteristic of ephemeral flowering plants in unpredictable habitats (Barbour et al. 1999), and *Vaucheria* seems to conform to this ecological strategy. The successful development of eight species in our severely desiccated mud samples from all four sites over extended time demonstrates a remarkable ability for survival by *Vaucheria* propagules to overcome an important environmental stress and be able to grow and succeed when conditions improve.

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NEW ENGLAND NOTE

WOODY *ARISTOLOCHIA* SPECIES IN WESTERN
MASSACHUSETTS

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Two woody pipevine (*Aristolochia*) species native to the southeastern and south central United States have been reported in Massachusetts. *Aristolochia tomentosa* Sims was first observed by Roberta Poland in 1957 in the vicinity of old cellar holes along the Connecticut River in Deerfield, Franklin County, and by 1983 was fully naturalized and spreading at this site (Burk 1984). A second, smaller colony of *A. tomentosa* was established by 1982 along a road edge in the Mount Tom State Reservation, Hampden County (Burk 1984). The origin of the Mount Tom population is unknown.

Aristolochia macrophylla Lam. was reported by Pfeifer (1966) from Essex County in the northeast corner of the state; whether *A. macrophylla* was naturalized at this site is uncertain, although Pfeifer noted that both *A. macrophylla* and *A. tomentosa* “may be grown in temperate gardens, chiefly as arbor or trellis subjects.” *Aristolochia macrophylla* is widely used in western Massachusetts as a screening vine, particularly on fences and verandas of wooden frame houses built in the late 19th century. Despite the highly specialized pollination syndromes in some members of the genus (Judd et al. 1999), observations in the Northampton, Massachusetts, area over a number of years indicate that *A. macrophylla* flowers and sets fruit freely in cultivation. Although single rampant pipevines may occasionally spread from fences or trellises onto nearby shrubs and trees, they do not usually escape and become naturalized in adjacent, seemingly suitable habitats such as overgrown vacant lots and wooded edges.

However, in October, 1997, a stand of *Aristolochia macrophylla* was encountered at the edge of moist hardwood forest in

Amherst, Hampshire County, by Tad Zebryk (*Zebryk 4273 MASS*). The Zebryk specimen apparently represents the first vouchered collection of *A. macrophylla* identified as naturalized in Massachusetts (Sorrie and Somers 1999). The plants occur at the intersection of Pine and State Streets in association with *Quercus rubra* L., *Q. velutina* Lam., *Fagus grandifolia* Ehrh., and *Fraxinus americana* L. On September 28, 1999, this population consisted of two groups of vines. One of these extended approximately 8 m along the north side of State Street, scrambling from the road edge over a cable railing and back an equal distance into the woodland. The group near the intersection with Pine Street contained fruiting vines that had climbed 7 m or more into a mature *Q. velutina* support tree. Tad Zebryk also observed a presumably naturalized population of *A. macrophylla* as early as 1994 in East Longmeadow, Hampden County. This population, which has since been extirpated, occurred with *Acer rubrum* L., *Betula populifolia* Marshall, *Rhus typhina* L., and *Rosa multiflora* Thunb. in early successional scrub near the remains of a former home site associated with an abandoned farm off Shaker Road.

Two additional naturalized populations of *Aristolochia macrophylla* have since been observed by C. J. Burk, one in Hampshire County and the other in Franklin County. During the summer of 1998, several widely spreading vines of *A. macrophylla* were seen in a strip of disturbed woody vegetation between Mass. Rt. 9 and the Mill River, 1.25 mi. (2.0 km) south of the center of Williamsburg, Hampshire County. Supporting trees included *Acer saccharum* Marshall, *Prunus serotina* Ehrh., *Quercus rubra*, and *Rhus typhina*. Individual stems of *A. macrophylla* extended 8 to 10 m up some support trees, and many of the tops and major vine-bearing branches of the support trees were observed to be severely bent or broken, either from the weight of the vines or winter storms or both. Entangled with the twining stems of *Celastrus orbiculata* Thunb., the vines formed four more or less distinct clumps of stems with two additional clusters 8 m distant to the north. Associated species included a dense stand of *Equisetum hyemale* L. beneath the larger group of vines, and abundant *Polygonum cuspidatum* Siebold & Zucc., near the northern cluster. The pipevines produced numerous fruits which had begun to split and release seeds by October 19, 1998; however no seedlings of *A. macrophylla* were evident in the vicinity. The site was re-examined on June 8, 1999, when the vines were flowering abun-

dantly. Since the initiation of growth in early spring, the vines had invaded a strip of vegetation which had been recently cleared during the course of road construction along Route 9.

A naturalized population of *Aristolochia macrophylla* was also observed by C. J. Burk in October, 1999, along Montague City Road, 55 m northwest of the intersection of Rastallis Street, in Montague, Franklin County. The vines occurred for a distance of 9 m along the roadside and extended from a recently mowed grassy strip into at least six support trees (three stems of *Rhus typhina*, two of *Fraxinus pennsylvanica* Marshall, and one of *Acer saccharum*) on an embankment abutting lowland forest. A residential neighborhood where *A. macrophylla* was grown as a garden ornamental was situated opposite the site along Montague City Road; the proximity of cultivated pipevines and the persistence of a clump of a *Hosta* cultivar at the site itself suggest that naturalized plants of *A. macrophylla* may have originated there from garden refuse, as woody pipevines propagate readily from ripened seed, softwood cuttings, root cuttings, and divisions (Wyman 1977). None of the naturalized vines seemed to have produced fruit in 1999. Specimens of *A. macrophylla* from the Williamsburg and Montague sites have been deposited in SCHN (Burk 98001, 99001).

To assess earlier predictions that *Aristolochia tomentosa* and *A. macrophylla* might be expected to spread in the region (Burk 1984), both known Massachusetts populations of *A. tomentosa* were revisited in 1998 and 1999. In 1983, the Deerfield population extended approximately 40 m along McClellan Farm Road on the west bank of the Connecticut River, overrunning woody vegetation from the road edge 15 m or more east past a group of old cellar holes to a ravine leading down to the Connecticut River (Burk 1984). By summer, 1999, the population had expanded south along McClellan Farm Road an additional 28 m. Seedlings of *A. tomentosa* also occurred in the herb stratum of floodplain forest on an upper terrace between the cellar holes and the river, with a few vines ascending support trees to the forest canopy. In the interval since 1983, both *Celastrus orbiculata* and *Polygonum cuspidatum*, invasive non-native species common in other Massachusetts floodplain forests (Kearsley 1999), had also become prominent at the Deerfield site.

Aristolochia tomentosa also persisted in the Mount Tom State Reservation through 1999, although clearing and cutting back of

vegetation along the road since the early 1980s has removed or reduced its principal supports. In September, 1998, the vines formed a loose ground cover for a distance of about 5 m along the road edge, extending back 3 m into adjacent forest. By late August, 1999, the colony had been reduced in size, largely by mowing and possibly by herbicide treatment along the road edge.

All extant populations of both *Aristolochia macrophylla* and *A. tomentosa* occur along wooded road edges adjacent to forested tracts; all but one are adjacent to stream banks. Unlike *Celastrus orbiculata*, the pipevines apparently do not strangle their support trees. However, because of their vigorous growth and apparent tendency to overrun and smother native woody vegetation at these Massachusetts sites, the status of both woody pipevine species should continue to be monitored.

ACKNOWLEDGMENTS. We are grateful to Ray Angelo, Tony Gola, and Paul Somers for information and helpful comments on the distribution of *Aristolochia* in Massachusetts and to Brita Dempsey and Robert McMaster for stalwart assistance in the field.

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NEW ENGLAND NOTE

DISCOVERY OF TWO NEW *LYCOPODIELLA*
(LYCOPODIACEAE) IN MAINE

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Lycopodiella Holub is a distinctive genus of wetland club-mosses. Species of this genus have creeping horizontal stems and upright, unbranched, leafy peduncles each of which may bear a single strobilus. Leaves of both the peduncle and strobilus (sporophylls) are unreduced and morphologically similar to the leaves of the horizontal stem, traits unusual in the family. The genus includes six species in North America, four widespread diploids and two tetraploids of global conservation concern (Wagner and Beitel 1993). Interspecific hybrids are common (Bruce 1975), and plants resulting from crosses between species of the same ploidy level are generally fertile, with normal spores, whereas those from crosses between species of different ploidy levels are sterile and produce aborted spores.

Three species of *Lycopodiella* occur in New England: *L. alopecuroides* (L.) Cranfill; *L. appressa* (Chapm.) Cranfill; and *L. inundata* (L.) Holub (Angelo and Boufford 1996). The former two species are found primarily on the Atlantic coastal plain and are more common south of New England. The latter species is a north temperate and boreal plant of North America and Eurasia. Both *L. appressa* and *L. inundata* are reported to occur in Maine (Angelo and Boufford 1996; Haines and Vining 1998), although *L. appressa* is currently ranked state historic (i.e., not observed extant in 20 years) by the Maine Natural Areas Program (1999).

Recognition of New England *Lycopodiella* is generally not problematic except where hybrid individuals complicate identification. *Lycopodiella inundata* is a small plant with upright shoots rarely taller than 6 cm. Its strobilus has spreading, entire sporophylls and commonly comprises 35–50% of the upright shoot height. *Lycopodiella appressa* is a taller plant with upright shoots 13–40 cm tall. Its strobilus has appressed, entire sporophylls commonly comprising 15–35% of the total upright shoot height. *Ly-*

copodiella alopecuroides, similar to the preceding species, is also a relatively robust bog clubmoss. Its upright shoots are 6–30 cm tall, of which the strobilus commonly comprises 15–35% of the total height. The sporophylls are spreading and provided with minute teeth on each margin. *Lycopodiella alopecuroides* has an unusual growth habit. The horizontal stems arch over the substrate and root at distant points where the stem contacts the ground. Both *L. inundata* and *L. appressa* have horizontal stems that are normally flat on the ground and root along the length. The reader is directed to Wagner and Beitel (1993) and Montgomery and Fairbrothers (1992) for additional characteristics that distinguish these three species of bog clubmoss.

On 29 November 2000, I conducted a preliminary rare plant and natural community survey on a property in Topsham, Sagadahoc County. Two open power-line clearings occurred on this property that have recovered as mixed graminoid–shrub wetlands in the low areas. These wetlands occur on saturated, sandy soils overlaid by a layer of organic matter and high bryophyte cover. Within one of these wetlands, a robust *Lycopodiella* with upright shoots exceeding 10 cm in height was observed. It had thick, arching horizontal stems, and leaves with minute teeth. Identification confirmed the small colony as a *L. alopecuroides* population of approximately six individuals. Species associated with the population included *Muhlenbergia uniflora* (Muhl.) Fernald, *Kalmia angustifolia* L., *Rhynchospora capitellata* (Michx.) Vahl, *Rubus hispidus* L., *Spiraea tomentosa* L., *Solidago uliginosa* Nutt., *Eriophorum virginicum* L., *Gentiana linearis* Froel., and *Lycopodiella inundata*.

A search of the area revealed a second colony of large *Lycopodiella* plants growing five meters from the previous location. The colony was substantially larger and grew across and along the edge of an infrequently used off-road vehicle path within the mixed graminoid–shrub wetland. Further examination revealed these plants as hybrids of *L. alopecuroides* and *L. inundata*. These hybrid plants exhibited the thick, arching stems of *L. alopecuroides* with the relatively tall strobili (35–46% of the total upright shoot height) of *L. inundata*. This morphology is similar to that observed in other *L. alopecuroides* $\times$ *L. inundata* occurrences of eastern North America (Montgomery and Fairbrothers 1992). The presence of hybrid plants is not surprising given the reproductive biology of *Lycopodiella* (i.e., frequency of hybridization in mixed

populations) and the abundance of *L. inundata* in the wetland. Neither *L. alopecuroides* nor its hybrid with *L. inundata* have been collected previously in Maine. Within New England, *L. alopecuroides* $\times$ *L. inundata* has only been reported for Massachusetts (Sorrie and Somers 1999). High-resolution digital scans of the collected plants were provided to James Montgomery to confirm species identification. Rare species report forms have been forwarded to the Maine Natural Areas Program and specimens of both taxa have been deposited in the University of Maine Herbarium.

Lycopodiella alopecuroides L. Cranfill. Sagadahoc Co.: Topsham, 29 Nov 2000, *Haines s.n.* (MAINE).

Lycopodiella alopecuroides $\times$ *L. inundata*. Sagadahoc Co.: Topsham, 29 Nov 2000, *Haines s.n.* (MAINE).

Prior to the November survey, the global range of *Lycopodiella alopecuroides* was reported to be Massachusetts, south along the coastal plain to Florida, and west to southeastern Texas, with disjunct occurrences in central Texas, Arkansas, and Kentucky (Wagner and Beitel 1993). This surprising discovery represents a range expansion of approximately 250 km north from the nearest known population in Winchendon, Worcester County, Massachusetts (Paul Somers, pers. comm.). In New England, *L. alopecuroides* is a *Flora Conservanda* Division 2 species (fewer than 20 New England occurrences; Brumback and Mehrhoff, et al. 1996) and therefore of regional conservation concern. In Massachusetts, it is provided a state status of endangered (Massachusetts Natural Heritage and Endangered Species Program 2000). In Connecticut, it has a state status of special concern, though it is believed extirpated (Connecticut Department of Environmental Protection 1998). In Rhode Island, it is given a state status of endangered (Brumback and Mehrhoff, et al. 1996).

Given its regional rarity, protection of the Maine station is a high priority for this species in New England. Prompt conservation action is suggested as vehicular traffic is currently damaging the hybrid plants proximate to the *Lycopodiella alopecuroides* colony. Maintenance of an open community for the power lines is likely to be beneficial to the survival of these plants. Future transmission-line tower repairs, however, could threaten the plants if heavy machinery is not routed around the colonies.

Coordination with Central Maine Power Company is crucial to the long-term survival of the *L. alopecuroides* occurrence.

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IN MEMORIAM

JOHN ALVORD CHURCHILL, M.D.

1920–2000

AN APPRECIATION



John Alvord Churchill was born 25 March 1920 in Boston, Massachusetts, the son of Alvord Barnes Churchill and Jean Adele Thompson Churchill. While John was a toddler his father finished law school and was encouraged to pursue a career in the growing city of Pittsburgh, so the family moved there. His parents were interested in nature, and at an early age he went with them on walks observing the plants and birds. He credits his earliest

interests in natural history as developing in the summer of 1925, when the family camped in a large tent in the woods on Goering Farm at Wexford, Allegheny County, Pennsylvania (about 30 miles from Pittsburgh). There he roamed in the woods and along a creek catching minnows. In 1926 he was taken touring in the family Dodge in New Hampshire, where his chief memory was of catching snakes. In 1929 a family friend returned from a hunting trip and brought him a dead Great Horned Owl that had been killed in a fight with a skunk. This he kept in a refrigerator until he could finish skinning and stuffing it. The refrigerator suffered from the experience, but John was not punished. We can all be grateful that John was not discouraged in his early endeavors at making natural history collections, because he became an enthusiastic and truly exceptional amateur botanist. At one time he aspired to collect a specimen of every vascular plant species in the United States. His extensive collections have been distributed throughout the United States and are of special note because of his interest in collecting rare plants and in establishing new distributional records.

John's earliest plant collections were obtained at Wexford in 1931, when he was 11 years old. Other early collections are from northern New Hampshire, where his family owned an old farm on Batchelders Brook, Warren Township, Grafton County. While in high school he had the opportunity to work with a number of botanists in the Botanical Society of Western Pennsylvania, especially John Bright, Charles Boardman, and John Wurdack (also a high school student at the time), who stimulated his interests in field work and botany. He also collected with Dr. O. E. Jennings of the Carnegie Museum of Natural History in Pittsburgh, who later authored *Wild Flowers of Western Pennsylvania and the Upper Ohio Basin*. By the time John entered Trinity College in 1939 he had already accumulated some 2000 herbarium specimens from western Pennsylvania and northern New Hampshire.

In 1930 John's father arranged for him to work in the Carnegie Museum on days when school was not in session. There, under the care of Reinhold Fricke, he was given a job of recording all the things that were in the crops and gizzards of a number of frozen Goshawks. These had been shot by farmers who received a bounty for the "chicken hawks" they killed. In the huge pile of extracted grasshoppers, mouse bones, and small-bird feathers there was no bit of a chicken. His results helped start the legis-

lation against killing hawks, owls, and eagles. A later assignment in the Museum was taking school children on tours around the museum and having them study the dioramas. This was his first taste of teaching, which he enjoyed and in which he saw a future. He also asked challenging questions of various members of the Museum staff, such as: why can it be seen from maps that the coasts of America seem to align with those of Europe and Africa and why do some small dinosaurs with small forelegs look like chickens? The money he earned he saved for trolley fare for getting to the Museum as frequently as possible.

John came up with the idea that it would be useful to put in some work in each specialty laboratory in the Museum. In botany he was associated with Dr. Jennings. Field trips of the Botanical Society of Western Pennsylvania enabled him to form a lifelong friendship with the late John Wurdack. This association stimulated his academic interests, resulting in the soaring of his school grades and, after skipping some grades, he graduated from Mount Lebanon High School in 1938.

One of John's early botanical exploits, in 1939 at age 19, was discovery of the rare species *Saxifraga aizoon* Jacq. and *S. cernua* L. on Mount Washington in New Hampshire. He was exploring a deep ravine cut into a flank of the mountain, and, while examining a cliff face, found *S. aizoon*, the first record for the species in New Hampshire. Frederic Steele (*Rhodora* 69: 485) noted that "... Dr. Churchill's discovery [of *S. aizoon*] was the most outstanding bit of botanizing on Mt. Washington in the past 50 years." Nearby on the mountain, John explored a shelf situated high in a vertical rock trough down which a cataract poured. On the shelf were some plants John assumed to be *S. rivularis* L., which is known from the Presidential Range. Nearly 30 years later Albion Hodgdon wanted to verify the *S. aizoon* record. John sent him a letter describing the area where it had been collected, and remarked that the shelf looked attractive but contained nothing unique, only *S. rivularis*. In 1967 Hodgdon and two colleagues found *S. aizoon* and inspected the rock trough. They decided they could not reach the shelf without undue risk, but did get close enough to use binoculars to examine the plants, discovering to Hodgdon's surprise that they seemed to have the features of *S. cernua* rather than *S. rivularis*. Subsequently the Churchill specimen in the Michigan State University Herbarium was examined critically and found indeed to be *S. cernua*, a principally

Eurasian species previously known in the conterminous United States only from northern Minnesota and the high mountains of Colorado.

John completed a pre-med program at Trinity College in Hartford, Connecticut, in 1942 and graduated from the University of Pennsylvania College of Medicine in 1945. While in medical school he met Dr. Edgar Wherry, who encouraged his botanical interests by including him on field trips. He also served in the U.S. Army, advancing from Private First Class to First Lieutenant. In 1946 he held a rotating internship at the Hospital of the University of Pennsylvania and in 1947 started training in neurology, as a Kirby-McCarthy Research Fellow. During this time he received a leave-of-absence to serve, at the invitation of Dr. Wherry, as physician for an expedition of scientists studying the biology of the Gaspé Peninsula. During this expedition he became acquainted with botanists Pierre Dansereau, Stanley A. Cain, W. H. Camp, N. C. Fassett, Hugh H. Iltis, N. Polunin, E. Rouleau, M. Raymond, and future Secretary of the Interior M. Udall. Stanley Cain later introduced John to W. Herb Wagner, whom John credited with teaching him new dimensions in biology. He participated in various of Wagner's "tornado-type" field trips and considered that some of the most important Michigan collections in his herbarium were made on these trips.

In 1948 John began a specialty in child neurology at Children's Hospital of Philadelphia and in 1950 became an assistant professor of neurology. He soon moved to the Montreal Neurologic Institute to complete training in EEG, and then started a private practice in neurology at Hartford, Connecticut. He also had a clinical appointment in neurology at the Yale School of Medicine. In 1953 he moved to Henry Ford Hospital in Detroit where he set up the first child neurology service in Michigan. In 1954 he was sent to Puerto Rico to survey the situation for developing a free breeding colony of macaques for the National Institutes of Health (NIH). In 1960 he went to England and Scotland to study children with cerebral palsy. In 1961 he was appointed associate professor of neurology at Wayne State University, and in 1967 was Chief of Pediatric Neurology of the Perinatal Research Branch of the National Institute of Neurological Diseases and Blindness (NIH) in Bethesda, Maryland. There he was faced with the difficult task of working out the methodology for analyzing neurological data, which he successfully solved. In 1972 he re-

turned to Wayne State University as full professor, working also in Detroit at the Lafayette Clinic, an agency of the Michigan Department of Mental Health. James Wells noted in a memorial address that John was revered as one of the best minds in neurology in the state of Michigan.

In 1981 John married Nadine Mitchell. John and Nadine formed a potent botanical team, and she participated extensively in his plant collecting activities. In 1983 he found working conditions in his department at Wayne State so rife with turmoil that he submitted his resignation. He and Nadine moved to Johnson City, Tennessee, where he took the position as professor of neurology in the new medical school of East Tennessee State University. The direction of this move may have been influenced as much by his desire to be intimately associated with the rich flora of the Southern Appalachians as with the escape from Detroit. The new position was linked with the Mountain Home Veterans Administration Hospital. In 1988, after the five years he had planned to spend in the position, he reduced his responsibilities in medicine to that of Clinical Professor at Eastern Tennessee State University and Consultant of Neurology for the Department of Health of the State of Tennessee. More or less simultaneously he increased his participation in botanical activities and in 1990 became a Voluntary Consultant in Botany for the U.S. Forest Service in Cherokee National Forest. In this role he served as the expert in locating rare species and identifying plants. From 1984 to 1994 he was the Appalachian Wildflower Celebration trip leader, and until very recently was the Roan Mountain Naturalists hike leader on their spring and fall rallies.

Although his professional duties in medicine left little time for his avocation in botany, John doggedly pursued his botanical interests throughout his entire medical career. In his memorial address, Jim Wells noted that John professed to know the Latin name of every plant in the United States. His labels, probably now familiar to virtually everyone who has studied herbarium specimens of this flora, have the heading "American Flora." While living in Michigan one of his active botanical pursuits was the study of the distribution of the sedge genus *Carex* in the state. He probably increased known county records for this genus by over 20% after the genus in Michigan was treated, in 1941, in a paper by F. J. Hermann. Churchill's contribution to our knowledge of *Carex* is evident from his collection of 482 specimens, includ-

ing 114 species and varieties, that were among the initial contributions of his herbarium to MSC in 1966.

That the Churchill Herbarium came to Michigan State University was something of a historical accident. John Beaman, then Curator of the Beal-Darlington Herbarium (MSC), was on leave in 1965–66 as a senior postdoctoral research fellow at the Smithsonian Institution. During that time he had returned briefly to Michigan and happened to be in the herbarium on a day that Churchill was visiting Warren Stoutamire, who was serving as Acting Curator of the Beal-Darlington Herbarium. In an informal chat, John more or less wondered out loud what he could do with his herbarium, which was getting too large for him to effectively manage. He recognized that his collection had grown to such importance and size that it should no longer remain a private possession, but rather should be generally available to scientists. Beaman suggested that it could be given to Michigan State University, and thus was initiated the contribution, which ultimately amounted to more than 30,000 specimens—by far the largest collection in the herbarium from a single donor. At the time of the first formal donation in 1966, about 6000 specimens were involved.

On a regular basis, generally two or three times a year, John shipped boxes of specimens to the Michigan State University Herbarium, the most recent received in 2000. Each carton was numbered, with more than 170 having been received over the years. The records show that 29,742 specimens had been accessioned by the end of 2000, but this is less than the total received, because for ten or more years records were not properly kept of the cryptogamic collections. He contributed at least 850 bryophytes, probably many more, and an unknown number of fungi, probably amounting to more than 1000. Most of his collections were made by himself or with his wife Nadine, but he also engaged in an active exchange program, which resulted in many collections from foreign lands, particularly Mexico, Guatemala, Chile, Canada, Sweden, China, and Siberia. Most likely every state in the United States is represented by one or more of his collections, but numerous collections are from Michigan, California, Hawaii, Pennsylvania, New Hampshire, Texas, and the southeastern United States. When he went to medical conventions, John managed to collect in the vicinity of those meetings. He also exchanged actively with other field botanists, with the

result that collections by botanists such as Duane Atwood, Bruce Bartholomew, Hal DeSelm, Paul Fryxell, Ron Hartman, Robert Kral, James Reveal, Tony Reznicek, and Dale Thomas are now among the Michigan State University Herbarium holdings. In some cases, John took the information from the labels of these collectors, and transferred it to his own labels. This practice can lead to some confusion if his labels are not read carefully.

John kept a record of every specimen he gave to the Michigan State University Herbarium, and maintained a continuing interest in the accuracy of the determinations. His policy was to send one specimen for each species, subspecies, or variety for each state. In the case of adventives, he sent only one specimen per species. In his active exchange with other collectors all the material he received as exchange was forwarded to MSC after the specimens had been studied and recorded for his files.

The Churchill specimens are noteworthy not only for their pure scientific value but also for their utility in teaching plant systematics at Michigan State University. They were carefully pressed and dried, with the leaves, flowers, and fruits arranged for most effective display when mounted. In graduate-level courses concerning the families of vascular plants, specimens are often selected from the main herbarium collection that illustrate family characteristics. It often has happened that Churchill collections are the very best ones, and occasionally the only ones, in the herbarium for this purpose. John once indicated that in his youth he had been trained by John Bright in the "press-in-the-wind" school, which meant carefully arranging the plants in the pressing papers at the time they were collected and drying them quickly to preserve as much color as possible.

In the 1970s John apparently decided that he had accomplished about all he could in collecting vascular plants in the United States. He therefore expanded his botanical activities in three directions, turning his attention first to bryophytes, then to fungi, and ultimately to lichens. Likewise he expanded his geographical horizons, traveling widely throughout the United States and even making one trip to Costa Rica, so that he could contribute tropical plants to the Michigan State University Herbarium. He used a copy of Grout's *Mosses with a Hand Lens and Microscope*, on loan from the Herbarium, for identifying his moss collections. He worked with Alex Smith at the University of Michigan to learn about fungi and was beginning to study lichens at the time of his

death. Thus far MSC has received 52 of his lichen specimens, but apparently more were collected.

Shortly before his death, John had completed the manuscript on which he had been working for many years for a book on "A Botanical History of Medicine of the Southern Appalachian Region." John wrote the text and his wife Nadine prepared the illustrations. The manuscript, organized by family, genus, and species, is 300 pages long and includes 125 species, all illustrated. Cherokee Indian uses of plants are emphasized. Sections include a preface, a consideration of today's traditional medicine and herbal medicine, plant classification, use of fish in tests for plant toxins, and references to major literature. In a letter of 28 January 1999 to Alan Prather, John worried that he might never find a publisher for the book because of the way it was put together. He noted that part of it is for a general readership and is mostly about Appalachian Mountain people's experiences with plants.

Among John's special interests in plants, combining botany and medicine, were the potential toxic properties of plants that might be eaten by humans. One project in this area concerned comparing fruits of the European *Sorbus aucuparia* L. with those of the native American species *S. decora* (Sarg.) C. K. Schneid. and *S. americana* Marshall. His hypothesis was that the European species contain more cyanide than do the North American species. On the basis of their knowledge of *S. aucuparia*, the Pilgrims apparently did not eat the fruits of the American species, as had been advised by the Indians. Had they done so, they might have avoided the scurvy they suffered. John used a cohort of minnows to test the relative toxicities, and also invented a device used to analyze the amount of cyanide in the species. A Churchill "principle" that came out of his research on toxic plants was that "prickly plants aren't toxic." One conclusion derived from his experiments on toxicity was that in the case of hardwood trees, the young leaves are more toxic than mature leaves. He felt that toxic substances in leaves were not merely the end products of metabolism, but were produced at an early stage of development.

His studies of potentially toxic plants resulted in some annotations on his herbarium labels that botanists, unaccustomed to such information on specimens, find quite memorable and sometimes amusing. For instance, on a specimen of *Angelica triquinata* Michx. [Churchill 86137 (MSC)] John made the following note: "Fish study: root 2.5 gm/dl – dead in 10', at 0.16 gm/dl –

stupefied long time.” John also tested ways to counter toxicity, as he reported from *Zizia aurea* (L.) W. D. J. Koch [Churchill 86219 (MSC)]: “in 2.5 gm/dl – sedated but revived in HOH. (Would have died if left).” No botanist will be surprised at the results from *Cicuta maculata* L. [Churchill 84173 (MSC)]: “Fish killed!”

About 23 years ago John had heart bypass surgery, which stood him in good stead, because he continued to live a most active life in both medicine and botany. In January 2000 he experienced chest pains suggesting the recurrence of heart problems. His cardiologist suggested that he should have another operation, but the prognosis for success was not very favorable. John was still in the process of finishing his book and decided that that objective was more important than taking a risk with surgery. In the summer of 2000 he finished the book. Nadine noticed that he did not look entirely well during that time, but John made no complaints. On September 14 he was taken to the hospital in Johnson City with what appeared to be a minor heart attack. A week later he experienced more serious difficulties and his condition deteriorated until his death on 18 November. He is survived by his wife Nadine, brother George, and daughter from a former marriage, Suzanne E. Churchill. With his passing both botany and medicine have lost a brilliant, dedicated, selfless, and indefatigable scientist, practitioner, and field botanist. He published about 50 papers in the area of medicine and the 11 botanical papers listed below. Among his greatest legacies, however, are the collection, organization, and donation of some 30,000 herbarium specimens that have been made available to botanists in perpetuity through donation of his herbarium to the Michigan State University Herbarium.

ACKNOWLEDGMENTS. Nadine Churchill graciously provided John's curriculum vitae, his portrait, and some supplemental information on his life that was instrumental in writing this tribute. E. G. Voss and an anonymous reviewer provided very constructive reviews of an earlier version of the manuscript.

BOTANICAL PUBLICATIONS OF JOHN CHURCHILL

CHURCHILL, J. A. 1937. New station of *Oxalis montana* forma *rhodantha*. *Rhodora* 39: 231.

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- . 1991. Addendum [*Juncus caesariensis* in Virginia]. *Castanea* 56: 223.
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- WAGNER, W. H., E. G. VOSS, J. H. BEAMAN, E. A. BOURDO, F. W. CASE, J. A. CHURCHILL, AND P. W. THOMPSON. 1977. Endangered, threatened, and rare vascular plants in Michigan. *Michigan Bot.* 16: 99–110.

—JOHN H. BEAMAN AND L. ALAN PRATHER, Department of Plant Biology, Michigan State University, East Lansing, MI 48824.

BOOK REVIEW

Gleason's Plants of Michigan: A Field Guide revised by Richard K. Rabeler. 1998 [corrected second printing February, 2001]. 398 pp. illus. ISBN 0-9663251-0-9 \$24.95 (Kivar® wear- and tear-resistant softcover). Oakleaf Press, Ann Arbor, MI.

This field guide is designed as a quick reference for the identification of the flowering plants and gymnosperms of Michigan. All the species in a particular genus are not keyed out, but the major ones are. The author indicates that plants in cultivation and those from difficult families are omitted, deferring to Voss's three-volume treatment of the flora of Michigan. The keys are intended to be used in the field, so the characters presented can be seen with the unaided eye or with a hand lens and a centimeter scale. The scale is provided at the back of the book.

There is a key to the four main groups of plants: trees, shrubs, or woody vines; unusual plants, including many aquatic plants; monocots; and herbaceous dicots. These keys eventually lead one to a plant family. Each family has a short description and then a key to the various genera. At the end of the key there is a designation as to where that taxon is to be found in the state. The acronyms for these regions are located on a map of Michigan.

There is an extensive bibliography of cited works and a list of other books useful in the identification of Michigan plants. There is a very useful section explaining the terminology used in the book, with accompanying line drawings. There are a number of illustrations, often depicting some special characteristic. Most taxa are not illustrated.

This is a very handy field guide, being a convenient size ($4\frac{3}{4} \times 8$ in.) to take in the field. The book is designed for persons having some background in plant identification; knowledge of the use of keys will help. This is a great field or lab key for the beginning student in a flora course, since it does not rely on illustrations. Most species that are commonly encountered in the field are covered. This book will be of use to anyone in north-eastern North America. I will consider requiring this for use in my plant systematics course.

—C. BARRE HELLQUIST, Biology Department, Massachusetts College of Liberal Arts, North Adams, MA 01247-4100.

NEW BOOKS

The Ecology of Trees in the Tropical Rain Forest by I. M. Turner. 2001. xiv + 298 pp. line drawings and black and white photos. ISBN 0-521-80183-4 \$80.00 (hardcover). Cambridge Tropical Biology Series, Cambridge University Press, New York.

E. Lucy Braun (1889–1971): Ohio's Foremost Woman Botanist. Her Studies of Prairies and their Phytogeographical Relationships by Ronald L. Stuckey. 2001. xxii + 240 pp. line drawings and black and white photos. ISBN 0-9668034-4-2 \$15.00 (hardcover). RLS Creations, Columbus, OH. [available from RLS Creations, Box 3010, Columbus, OH 43210; include \$2.00 s&h]

The European Garden Flora: A Manual for the Identification of Plants Cultivated in Europe, both Out-of-Doors and Under Glass. Volume VI. Dicotyledons (Part IV) Loganiaceae to Compositae edited by J. Cullen, J. C. M. Alexander, C. D. Brickell, J. R. Edmondson, P. S. Green, V. H. Heywood, P.-M. Jørgensen, S. L. Jury, S. G. Knees, H. S. Maxwell, D. M. Miller, N. K. B. Robson, S. M. Walters, and P. F. Yeo. 2000. xv + 739 pp. line drawings. ISBN 0-521-42097-0 \$175.00 (hardcover). Cambridge University Press, New York.

Flora Europaea on CD-ROM. 2001. CD-ROM interactive software. ISBN 0-521-77811-5 \$550.00. System requirements: IBM PC or compatible, minimum 80486 processor, 4 MB free RAM, VGA monitor or better (800 × 600 pixel resolution). Win 9× operating system. Windows compatible CD-ROM drive and Microsoft CD-ROM extensions (MSCDEX) version 2.0 or higher. Cambridge University Press, Port Chester, NY.

Gleason's Plants of Michigan: A Field Guide revised by Richard K. Rabeler. 1998 [corrected second printing February, 2001]. 398 pp. illus. ISBN 0-9663251-0-9 \$24.95 (Kivar® wear- and tear-resistant softcover). Oakleaf Press, Ann Arbor, MI.

Guide to Standard Floras of the World, 2nd Edition by David G. Frodin. 2001. xxiv + 1100 pp. ISBN 0-521-79077-8 \$240.00 (hardcover). Cambridge University Press, New York.

NEBC MEETING NEWS

June 2001. The June “away” meeting was held at Bennington College in Bennington, Vermont. Paul Somers introduced the evening’s speaker, Dr. Kerry Woods of Bennington College, whose topic was “The imagined forest: Stability and change in old-growth hemlock–northern hardwoods.” The current concept of “old-growth forest” that controls conservation policy in the northeast is of a stable, old, undisturbed forest dominated by endogenous factors—processes internal to the community. However, we have no measurable or observable property that serves as an indicator that a community is “old growth” according to this definition. Kerry contends that our definition of “old-growth forest” and its dynamics is based on unverified models and untested assumptions—and that “old growth” really is only an imaginary forest.

To determine the actual dynamics of old forest communities, Kerry is studying two forests in northern Michigan that appear to have been free of major disturbance for at least 500 years. His study at both sites compares modern forest composition with data from plots established in 1962 (the Huron Mountain site) and 1935 (the Dukes Forest site). His data show that, at both sites, sugar maple is increasing; hemlock stable or increasing; birch significantly decreasing; and beech (which only arrived at the Dukes Forest site about 500 years ago—first generation trees are still standing) significantly increasing. Birch appears to have become established following some historic disturbance around 250 years ago, and is now not replacing itself. Beech has an age-distribution curve skewed to young trees. At the Dukes Forest site, the basal area of beech has increased by 2 to 4 times since the initial data collection 60 years ago.

The data show that these old forests are in fact not stable communities, but are undergoing slow successional changes in response to historic exogenous disturbance events. Community composition is still changing in response to events that occurred more than 200 years ago! Kerry’s model predicts that a steady state, if ever reached, would be dominated by hemlock and beech, but that this state would be reached very slowly since hemlock requires 2 to 3 generations (1000 to 2000 years) to reach dominance. Kerry concluded that the current old-growth forest concept is not supported by this research, and suggested that forest con-

servation policy should be revised to reflect the actual, if slow, dynamics of old hemlock–northern hardwoods forests.

—LISA A. STANDLEY, Recording Secretary *pro tempore*.

June 2001 Field Trips. Fifteen members and guests met at 2 pm on a hot Friday afternoon, June 8, to explore the area in Pownal, Vermont, known as Krigger Rocks, with Dr. Kerry Woods as leader. Starting at Rt. 346, a peculiar rush, later identified as *Juncus compressus*, was found thriving in the salted road shoulder. Climbing gently up an old quarry access road, President Lisa Standley pointed out reed-like sedge, *Carex sparganioides*. The group fanned out upon entering the quarry proper, with various members pointing out plants of interest, most of them calciphiles and many of them rare in Vermont. Such plants as *Asplenium ruta-muraria*, *Cystopteris tenuis*, *Carex aurea*, *C. eburnea*, *Arabis lyrata*, *Rhus aromatica*, *Cornus rugosa*, and *Campanula rotundifolia* were seen around the quarry edges. On quarry spoil were fine plants of the native *Celastrus scandens* in full flower, a treat for those used to seeing only the increasingly invasive alien, *C. orbiculatus*. *Potentilla arguta*, *Penstemon hirsutus*, and *Quercus muhlenbergii* were noted here as well. The dry limestone woodlands above the quarry yielded *Asclepias quadrifolia* (in fine bloom), *Aureolaria flava* (young foliage only), and *Conopholis americana*. These were mixed with the usual and common members of the local flora such as *Carex pensylvanica*, *Hepatica americana*, and *Solidago caesia*. After two hours of relaxed botanizing, members strolled back to their cars and headed for well-deserved cooling refreshments, a quick cleanup, and supper.

On Saturday June 9, 12 Club members ventured out of New England into the wilds of New York. Led by Kerry Woods, the group explored the ledges and ravines of The Notch, in White Creek, New York (Washington County). The forests and ledges on the east side of the valley support a very rich herbaceous flora that includes *Laportea*, *Hepatica*, *Dentaria*, *Hydrophyllum*, *Dicentra*, *Allium*, *Caulophyllum*, *Claytonia*, violets, and other forbs. The fern flora is equally rich, with Goldie's fern in abundance, along with *Deparia acrostichoides* and *Diplazium pycnocarpon*. The forests and ledges on the west side of the valley are drier, with a chestnut oak (*Quercus montana*) woods at the summit and

surprising hemlock–yellow birch swamps in depressions on the ridge. In perfect weather, the group enjoyed the ledge scrambles, fresh black bear tracks, and wonderful views extending from Mount Greylock to Dorset.

—ARTHUR V. GILMAN, Field Trip Chair.

September 2001. The September “away” meeting was held at the Waquoit Bay National Estuarine Research Reserve in Falmouth, Massachusetts. Vice President Paul Somers introduced the evening’s speakers, Dr. Richard Backus and Pamela Polloni, our hosts from the Botanical Club of Cape Cod and the Islands (BCCCI). Dr. Backus, Curator Emeritus of the herbarium at the Marine Biological Laboratory (MBL), specialized in ichthyology throughout much of his career and retired as Senior Scientist of the Woods Hole Oceanographic Institution. Since his retirement he has been working on the flora of Falmouth, Massachusetts. Pam, Acting Curator of the MBL herbarium, is a consulting botanist with the Massachusetts Natural Heritage and Endangered Species Program. Their topic was “The Floral History of Penikese Island.”

Penikese is a 75-acre island in the Elizabeth Islands chain off Cape Cod, owned by the Massachusetts Division of Fisheries and Wildlife. Currently, it is occupied by the Penikese Island School for troubled boys, as well as a large nesting colony of gulls and terns and one of the state’s two nesting colonies of Leach’s storm petrels. In the 1800s, sheep, turkeys, and rabbits were raised on the island, and it housed the short-lived Anderson School of Natural History, founded by Louis Agassiz in 1873.

One of the first persons to describe Penikese Island was Gossnold, following his expedition of 1602. He described the island as being covered with cedars, some of which were cut by members of his party. David Starr Jordan, later president of Stanford University, wrote the first flora of Penikese in 1873, and described the island as “absolutely treeless and nearly shrubless . . . about as barren looking a pile of rock and stone as one could well imagine.” Nonetheless, Jordan recorded 114 species of vascular plants. Subsequent floristic surveys were undertaken in 1923, 1947 (149 species), and 1973 (160 species). The current study is based on field work conducted in 1998 and 1999. The flora currently stands at 219 species, of which 47% are aliens.

The principal change in the flora of Penikese appears to be the increasing diversity and dominance of shrubs and vines since the cessation of grazing; nine new species became established on the island in the 50 years between 1923 and 1973. Interestingly, the first record of poison ivy was in 1947, and red cedar was first observed to return to the island in 1999. Currently, 80–90% of the island is covered by woody shrubs and vines but there are no ericads or grapes on the entire island. Other interesting observations made by the team include the loss over time of fern diversity. Hay-scented fern was a dominant species in 1923 and is currently restricted to a single plant. Marsh fern, once abundant around the ephemeral ponds, had disappeared by 1960.

The current floristic survey has revealed many possibilities for further study, particularly in the realm of disturbance and ecological succession. Dr. Backus predicts, in the absence of disturbance, an eventual return to the red cedar landscape recorded by Gosnold. The presenters suggest controlled burns for managing aggressive shrubs and woody vines and for encouraging native grasses, which might also improve nesting sites for seabirds.

September 2001 Field Trips. About 20 Club members and friends participated in a Friday afternoon tour of Crane Wildlife Management Area (Crane WMA) and Waquoit Bay National Estuarine Research Reserve (Waquoit Bay NERR) in Falmouth. Paul Somers, Maile Neel, and Pamela Polloni interpreted research being conducted on habitat restoration for *Agalinis acuta*, the federally endangered sandplain gerardia. Starting at Crane WMA, the group examined flowering and fruiting plants of *A. acuta* in and adjacent to plots established in December 1997. The 1998 results showed that grassland plots prepared for seed sowing by burning of thatch, soil scarification and removal of thatch, or burning followed by soil scarification each produced significantly more *A. acuta* plants than control plots. Maintenance of the experimental area by spring mowing in 1999 and 2000, and burning in 2001, has resulted in a gradually increasing and spreading population. Two highlights of the botanical exploring in the area were the discovery of a new colony of *Agalinis* to the north of the experimental area and a healthy population of *Scleria pauciflora* var. *caroliniana*, a state-listed rare species not previously known from Crane WMA. At Waquoit Bay NERR, a series of smaller experimental plots that preceded the Crane WMA plots were ex-

amined and discussed. These research plots tested seed banking and management by burning, scarification, and mowing on a smaller scale. The seed bank plots have revealed that *A. acuta* can seedbank for at least four years. At Waquoit, Maile Neel discussed pollination studies she initiated there in 2000. Her study, using bagged flower buds, has demonstrated that *A. acuta* is capable of a very high level of selfing but that seed set is typically lower than when cross pollination occurs. Today a population with over 30,000 plants is being maintained by winter and spring mowing at the experimental site. The group also visited a neighboring cemetery where a portion is being managed for sandplain gerardia.

On a beautiful, early fall Saturday morning, 20 Club members toured the Mary Dunn coastal plain pond complex in Hyannis, led by BCCCI member and founding president, Mario DiGregorio. Mario and the Nature Conservancy hydrologist Rich McHorney provided a history of the botanical exploration of the ponds and an explanation of their unique hydrology. The group foraged around the pond edges and was rewarded with *Coreopsis rosea*, *Drosera filiformis*, *Eleocharis melanocarpa*, *E. robbinsii*, *Lachnanthes caroliniana* in fruit, *Panicum wrightianum*, *Polygala cruciata*, *Rhynchospora macrostachya*, *Scleria*, and *Stachys hyssopifolia*. One late-blooming *Sabatia kennedyana* was found. After lunch, current BCCCI president Don Schall led 12 botanists on a walk at Sandy Neck beach in Barnstable. The interdunal swales contained small cranberry-dominated wetlands with *D. filiformis*, *Euthamia tenuifolia*, *Pogonia ophioglossoides*, and *Lycopodium appressum* present, and with *Carex silicea* at the fringes. The nearby salt marsh was distinguished by *Pluchea* in full bloom, *Scirpus robustus*, and *Aster subulatus*. Several handsome specimens of *Panicum amarum* were found near the marsh edge.

—LISA A. STANDLEY AND PAUL SOMERS, Recording Secretaries *pro tempore*.

REVIEWERS OF MANUSCRIPTS

2000–2001

The Editor-in-Chief of *Rhodora* is grateful to the members of the editorial staff and to each of the following specialists for their participation in the review process. Their conscientious and thorough evaluation of manuscripts helps to maintain the quality of this journal.

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